SONGBIRD COMMUNITY ECOLOGY AND HABITAT SELECTION IN THE CHICAGO AREA

BY

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THESIS

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Abstract

Urbanization has considerable effects on native flora and fauna, and is likely the most important driver of extinction. Two major stressors that have been shown to strongly impact wildlife communities in urban areas are habitat loss and fragmentation, which expose organisms in remnants to increased stressors associated with edges. Another potential stressor is the encroachment of invasive vegetation. Invasive plants are highly successful colonizers of natural habitats within urban environments, yet their impacts on native fauna remain largely unknown. I was interested in examining how these stressors impacted bird communities. Specifically, I addressed two questions: (1) how do exotic shrub invasions impact woodland songbirds within urban landscapes? and (2), how do bird communities change across forest-suburb boundaries? Field work was conducted in the Chicago metropolitan area during the breeding seasons of 2010 and 2011. I found that even though measures of invasive vegetation were only weakly correlated with avian community structure (i.e. a matrix of all species and their relative abundances at each plot), both species richness and the conservation value of birds within a plot decreased with an increase in European buckthorn (*Rhamnus cathartica*) tree dominance. I also found that birds that nest and forage in the upper canopy showed negative responses to shrub invasion, while understory species such as the northern cardinal (*Cardinalis cardinalis*) showed positive responses. Regarding forest-suburb edges, I found that whereas forest bird community composition changed with distance from the edge, the suburban bird community remained homogenous throughout. Similarly, the densities of the most common forest species increased with distance from the edge, while the densities of the most common suburban species fluctuated in a seemingly random fashion with distance from the edge. Lastly, I found evidence that the northern cardinal could be classified as an edge-exploiter. Overall, this research adds to our

understanding of the ways that management practices can influence avian responses to local vegetation structure and landscape in metropolitan environments.

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Chapter 1

General Introduction

Human alteration of the earth's ecological processes is tremendous and growing (Vitousek et al. 1997). A world-wide trend of increasing urban sprawl (United Nations 2008) is concerning to ecologists because habitat loss is widely recognized as the greatest threat to biodiversity and imperiled species (Wilcove et al. 1998). Urbanization has been shown to be one of the leading causes of extinction and biotic homogenization, which is the increase in dominance of a few synanthropic species at the expense of native diversity (McKinney 2006). While conservation biologists have often focused on the protection of "natural" areas experiencing relatively little human impact, the conservation of native biodiversity has recently emerged as an important priority in urban areas (Miller and Hobbs 2002). Urban parks for example, can have relevant conservation value because they can serve as wildlife reservoirs in developed areas (Fernández-Juricic 2001).

The impacts of urbanization on avian communities have been well documented (Marzluff 2001, Chase and Walsh 2006). When forests are replaced with urban land cover, bird communities rapidly lose diversity (Wilcove 1985). Populations of birds remaining in native fragments, such as forest patches, are threatened by increased disturbance and mortality due to human activity, exposure to larger populations of parasites and predators, and changes in resource availability and trophic structure (Marzluff and Ewing 2001). Another stressor that could possibly impact bird communities is the invasion of exotic plant species, which are particularly successful colonizers of natural remnants within urban landscapes (Borgmann and Rodewald 2005). Understory structure may be the most important factor in avian habitat

selection (Cody 1985), so dense monotypic stands of invasive shrubs may play a large role in structuring bird communities.

Overall, while the avifauna of forests have fared better than birds associated with other habitats such as grasslands, many neotropical migrants that breed in these forests have experienced severe declines (Robbins et al. 1989, Askins et al. 1990). More recently, analyses of combined Breeding Bird Survey and Audubon Christmas Bird Count data have revealed that many common birds are also experiencing steep population declines (Butcher and Niven 2007). For example, the common grackle (*Quiscalus quiscula*), an abundant and widespread urban bird, experienced a 61% population decline between 1965-2005 (Butcher and Niven 2007).

Compared to other topics in urban avian ecology, relatively little is known about how the urban matrix influences bird community structure within forest fragments and even less is known about how these fragments influence bird communities within the urban matrix. Additionally, little is known about avian responses to hard suburban-forest edges, despite their ubiquity in urbanized landscapes. The impacts of ecotones on avian communities have received considerable attention, yet few studies have examined how bird populations change on both sides of an edge between distinct habitat types. It is also unclear how the spread of certain invasive shrub species impacts bird communities, particularly within urbanized landscapes. Ecologists have called for research that examines the effects of invasives and their removal on native avifauna to help inform the management of woodland habitats (Knight et al. 2007). My research has focused on addressing these gaps in knowledge by studying bird communities in the suburbs of Chicago, Illinois. Results from this research will advance our understanding of urban avian ecology and conservation, and will hopefully influence future land-management choices.

Thesis Organization

This thesis is organized into the following three chapters: Chapter 2 examines how bird communities respond to exotic shrub invasions. Chapter 3 investigates how bird assemblages change along a forest-suburb edge. Chapter 4 summarizes conclusions and points out limitations from this research. Study design, data collection, statistical analyses, and preparation of the text were the responsibility of the M.S. candidate, while guidance and editorial advice were given by the advisor Dr. James R. Miller.

References

Askins, R. A., J. F. Lynch, and R. Greenberg. 1990. Population declines in migratory songbirds in eastern North American. Current Ornithology 7: 1-57.

Borgmann, K. L., and A. D. Rodewald. 2005. Forest restoration in urbanizing landscapes: interactions between land uses and exotic shrubs. Restoration Ecology 13: 334-340.

Butcher, G. S., and D. K. Niven. 2007. Combining Data from the Christmas Bird Count and the Breeding Bird Survey to Determine the Continental Status and Trends of North America Birds. National Audubon Society.

Chase, J. F., and J. J. Walsh. 2006. Urban effects on native avifauna: a review. Landscape and Urban Planning 74: 46-69.

Cody, M. L. 1985. An introduction to habitat selection in birds. In: Cody, N. L. (Ed.), Habitat Selection in Birds. Academic Press, Orlando, pp. 4-56.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology and Systematics 34:487-515.

Fernández-Juricic, E. 2001. Avian spatial segregation at edges and interiors of urban parks in Madrid, Spain. Biodiversity and Conservation 10: 1303-1316.

Knight, K. S., J. S. Kurylo, A. G. Endress, J. R. Stewart, and P. B. Reich. 2007. Ecology and ecosystem impacts of common buckthorn (*Rhamnus catartica*): a review. Biological Invasions 9: 925-937.

Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds. Chapter 2 in eds, J. M. Marzluff, R. Bowman, and R. Donnelly, Avian Ecology and Conservation in an Urbanizing World. Kluwer Academic Publishers, Boston, MA. Pages 19-47.

Marzluff, J. M., and K. Ewing. 2001. Restoration of fragmented landscapes for the conservation of birds: a general framework and specific recommendations for urbanizing landscapes. Restoration Ecology 9: 280-292.

Miller, J.R., and R. J. Hobbs. 2002. Conservation where people live and work. Conservation Biology 16: 330-337.

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation 127: 247-260.

Robbins, C. S., J. R. Sauer, R. S. Greenberg, and S. Droege. 1989. Population declines in North American birds that migrate to the neotropics. Proceedings of the National Academy of Sciences of the United States of America 86: 7658-7662.

United Nations. 2008. World Urbanization Prospects: The 2007 Revision Population Database. [online] URL: http://esa.un.org/unup/. Accessed 2-20-12.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillio. 1997. Human domination of earth's ecosystems. Science 277: 494-499.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66: 1211-1214.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. Bioscience 48: 607-615.

Chapter 2

Assessing the Responses of Woodland Songbirds to Exotic Shrub Invasions in the Chicago Area

Abstract

The encroachment of invasive plants is quite extensive throughout the forest understories of the midwestern United States and consequently, restoration efforts often focus on the removal of these invasives. Whereas the negative impacts of invasives on native plant communities are well-documented, the effects on native fauna remain largely unknown. To address this issue, we examined the response of avian communities to invasive plants such as European buckthorn (*Rhamnus cathartica*) in the Chicago metropolitan region. During the 2010 and 2011 breeding seasons, we surveyed avian communities in 46 forest plots representing a gradient of exotic vegetation invasion, ranging from little to severe infestation. In addition, vegetation structure and composition were quantified at all survey plots, as was the landscape context in which these plots were embedded. Results demonstrated that both species richness and conservation value (an index that assigns higher values to areas with greater numbers of species of conservation concern) decreased with an increase in buckthorn tree dominance. However, measures of invasive vegetation were only weakly correlated with avian community structure, indicating that other environmental variables were more important in this regard. We also found that species that nest and forage in the upper canopy showed negative responses to invasion, whereas understory species showed positive responses. Overall, this research will add to our understanding of the ways in which non-native plant invasions can influence avian responses to local vegetation structure and landscape context. While buckthorn removal would likely increase

species richness and conservation value, species-specific responses to invasion should be taken into consideration when developing restoration plans.

Introduction

Negative impacts of invasive species on ecosystem functioning and native biodiversity have emerged as top conservation issues (Wilcove et al. 1998, Pimentel et al. 2000). Invasive plants can alter nutrient cycles, hydrology, and fire regimes, and also outcompete native species (Mack et al. 2000). Recently, however, some ecologists have advocated species assessments based on their environmental impact rather than their origins (Davis et al. 2011), as the ecological impacts of non-native invasives are not exclusively negative. For example, some invasive plants may have positive effects on native species via habitat modification (e.g. invasive shrubs can provide nesting or perching structures for birds) or the provisioning of additional food in resource-limited habitats (e.g. fruigivores and omnivores can benefit from fruit growing on invasive vegetation; Reichard et al. 2001). To properly inform land managers about the costs and benefits associated with eradication programs, a better understanding of the potential consequences associated with biological invasions is needed.

One area of research that has received relatively little attention is the impact exotic plant invasions are having on bird populations and communities. For many birds, understory structure may be the most important factor in habitat selection (Cody 1985). Studies that have addressed the effects of shrub invasions on avian community structure have found that avian species richness (Ellis 1995, Frost and Powell 2011), diversity (Hunter et al. 1988, Germaine et al. 1998), and abundance (Hunter et al. 1988, Ellis 1995, Germaine et al. 1998) are generally lowest in heavily invaded areas. Additionally, over-wintering fruigivorous birds have been observed in

higher densities in forested areas with invasive shrubs than in uninvaded areas (McCusker et al. 2011). Species such as the American robin (*Turdus migratorius*) and cedar waxwing (*Bombycilla cedrorum*) can thus facilitate further spread of invasives as they disperse (Bartuszevige and Gorchov 2006). Other studies that have investigated interactions between birds and invasive vegetation have examined changes in nesting success. For example, several researchers have found that birds nesting in invasive shrubs can experience higher nest predation (Schmidt and Whelan 1999, Borgmann and Rodewald 2004) and brood parasitism rates (Borgmann and Rodewald 2004) than those nesting in native shrubs. In some instances, invasive shrubs appear to act as ecological traps (Schmidt and Whelan 1999, Rodewald et al. 2010).

Surprisingly, the impacts on avian communities by one particularly dominant and widespread invasive shrub, European buckthorn (*Rhamnus cathartica*; hereafter buckthorn), have been largely ignored. Native to North Africa and Eurasia, buckthorn was introduced to North America as an ornamental shrub in the late 1880s because it was desirable for hedges (Godwin 1943). In the early 1900s, buckthorn became naturalized throughout much of the upper midwest and northeastern United States, displacing populations of native flora (Godwin 1943). Buckthorn has recently been implicated as the primary driver of an extensive "invasional meltdown" because it facilitates the invasion of other exotic species, including the European earthworm (*Lumbricus terrestris*; Heimpel et al. 2010). To our knowledge, there have been no studies that have examined the impacts of buckthorn invasion on avian communities in the peer-reviewed literature, although several technical reports have noted that forests heavily invaded by buckthorn support lower avian abundance (Meister 2006) and species richness than uninvaded forests (Apfelbaum and Haney 1991, Meister 2006).

To fill this gap in knowledge, we quantified shifts in avian community structure with increasing amounts of buckthorn using a gradient approach in forest remnants in the Chicago metropolitan area. The removal of invasive woody plants is a primary restoration strategy in Chicago area forest preserves, intended to improve habitat conditions for native species (Meister 2006, Smith and Gehrt 2010). The goal of our study was to determine if invasive vegetation diminishes habitat quality and poses a threat to the conservation of woodland songbirds in a highly fragmented, human-dominated landscape. Specifically, we addressed the following questions: (1) how do measures of invasive vegetation correlate with avian community structure? (2) How are these patterns mediated by other local and landscape-level variables? (3) How do individual species, particularly those of conservation concern, respond to invasive vegetation, as well as other local and landscape variables?

Methods

Study area

We conducted fieldwork on publicly owned land in Cook, Lake, DuPage, and McHenry counties in the Chicago metropolitan area (Fig. 1). Oak (*Quercus* spp.), hickory (*Carya* spp.), elm (*Ulmus* spp.), and ash (*Fraxinus* spp.) were the most common native tree species and understories were dominated by invasive shrubs including buckthorn, Amur honeysuckle (*Lonicera maackii*), and Multiflora rose (*Rosa multiflora*). In northeastern Illinois, buckthorn is the most dominant invasive shrub, as well as the most common tree species in the Chicago metropolitan area (McPherson et al. 1997). Historically, these forests were subjected to frequent fires that maintained relatively open stands with less structural diversity (Sullivan 2011). But with settlement in the early 1800s came fire suppression, which allowed for the successful invasion of

nonnative shrubs (Sullivan 2011). These invasive plants can create such dense shade that they kill native understory plants and prevent oak regeneration (Knight et al. 2007).

Invasive plants are highly successful colonizers of natural habitats within urban environments (Borgmann and Rodewald 2005) due to increased seed movement and disturbance (Hobbs 2000). Habitat loss and fragmentation, common features of urbanized landscapes, also increases light availability at edges, providing ideal conditions for invasive plant establishment (Matlack 1993). Buckthorn's proliferation is attributed to high fecundity, rapid growth, seedling success in disturbed areas, shade tolerance, high photosynthetic rates, its wide tolerance for drought and moisture, and its bird-dispersed fruit (Knight et al. 2007). For these reasons, invaded areas can rapidly be transformed into dense monotypic buckthorn stands. As a result, management practices in the Chicago area's forest preserves tend to focus on invasive species removal via cutting and herbicide application as well as prescribed burning, and tree removal to reduce canopy cover (Smith and Gehrt 2010).

Site selection

A total of 46 one-ha plots in 34 forest preserves were selected to represent a gradient of invasive species abundance. Whereas some preserves were heavily invaded with exotic vegetation throughout, a few plots remained uninvaded, and others were composed of a mosaic of patches in which the invasive plants had been removed at varying time intervals (Umek 2009, S. Cleeton *personal observation*). While there were multiple plots within some forest preserves, all plot centers were at least 400 m apart and represented different levels of invasion, so they were therefore considered independent sampling units. The woodland fragments in which these plots were embedded ranged from 8-619 ha and averaged 95.5 ha in size.

Thirty-five of the plots were originally included in an ongoing study of the effectiveness of biodiversity management practices in the Chicago metropolitan area (Umek 2009). In each of the four counties land managers were asked to provide plots representative of four different restoration categories: degraded, recent management (areas that have been undergoing restoration for < 7.5 years), mature management (areas that have been undergoing restoration for ≥ 7.5 years), and "high-quality". No restoration was planned for the duration of the study in the forest plots that were considered degraded (Umek 2009). Overall, there was a considerable amount of variability with respect to measures of invasion within the restoration categories, and after analyzing these differences statistically we decided not to use the categories in further analyses but rather take a gradient approach. This suite of plots was supplemented with an additional 11 plots which also represented varying degrees of invasion.

Bird surveys

We surveyed bird communities three times annually between late May and early July in 2010 and 2011 using standard point count methodology (Ralph et al. 1993). We conducted 10-minute unlimited distance point counts on clear mornings between sunrise and 0930 hours. During each survey we recorded all birds seen or heard as well as distances of birds from the plot center (Buckland et al. 2001). All plot centers were > 400 m apart to minimize double counting. Surveys were conducted by two observers each year, and observers rotated among points to minimize potential observer bias. Prior to each field season, observers underwent a week-long training period to sharpen identification and distance estimation skills.

Vegetation sampling

Vegetation surveys at each plot were adapted from the BBIRD field protocol (Martin et al. 1997). Vegetation was measured at four sampling locations nested within each plot: one at the plot center and three at locations 30 m from the plot center. The compass direction of the first outer vegetation sampling location was chosen at random, and the other two locations were placed at 120° in either direction. We measured vegetation within a 5-m and an 11.3-m radius sub-plot centered at each sampling location. Within the 5-m sub-plot we measured litter depth, shrub structure and composition, and percent ground cover. All woody stems > 1 m in height were identified to genus or species. Woody plants were classified as shrubs if the diameter at breast height (dbh) was < 7 cm or as trees if the dbh was > 7 cm. The height and width of each shrub were also measured and shrub cover was estimated visually. To quantify overall ground cover, we randomly placed a 1 x 1-m quadrat in each of the 5-m sub-plots and estimated percent grass, forb, litter, and bare ground using the Braun-Blanquet Cover Abundance Scale (Ralph et al. 1993). In each 11.3-m sub-plot, we counted the total number of trees (by species) and snags, and recorded the smallest and largest tree dbh.

Landscape variables

Landscape composition surrounding each plot was quantified using 2009 high-resolution satellite imagery obtained from the World Imagery basemap in ArcGIS 10 (Environmental Systems Research Institute, Redlands, CA). We delineated the forest remnants in which the plots were embedded and calculated the perimeter of the remnant (m) and total contiguous forested area (ha). We also measured the distance between each plot center and the nearest edge (m) to account for potential edge effects (Laurance and Yensen 1991). Within 1,000 m of the plot

center, we calculated building density, and the percentage of forest, agricultural, and urban cover.

Data analyses

We restricted analyses to bird species that typically breed in the area. Additionally, we excluded gulls, raptors, shorebirds, and waterfowl because point counts are not considered a suitable method for these taxa (Bibby et al. 2000). Point count data were truncated at 50 m for all analyses to maximize the probability that bird counts reflect the vegetation measured at the plot (Martin et. al 1997) and because a few plot centers were not much further than that to an edge and detection probabilities generally decrease with increased distance from an observer.

Prior to data analysis, we removed environmental variables that were redundant or strongly correlated ($r > 0.70$). For example, forest patch perimeter and forested area were highly correlated ($r = 0.78$), so we dropped perimeter from further analyses because our measure of distance-to-nearest-edge is useful in quantifying edge effects. These procedures resulted in the inclusion of eight plot-level variables and six landscape-level variables (Table 1). Of the local variables three were direct measures of invasion and two were indirect measures of invasion: tree density, which was positively correlated with the proportion of buckthorn trees ($r = 0.53$), and bare ground cover, which was positively correlated with both tree density ($r = 0.44$) and the proportion of buckthorn trees ($r = 0.43$). Rapid litter decomposition can lead to bare ground conditions beneath buckthorn stands (Knight et al. 2007). Species which forage by probing for soil-dwelling invertebrates may benefit from greater access to bare ground (Perkins et al. 2000). We also included leaf litter cover as an additional ground cover variable. Increased leaf litter is important for ground nesting birds because it may improve nest concealment (Mattsson and

Niemi 2006), and for ground foraging birds that consume litter-dwelling arthropods (Haskell 2000). Lastly, snag density was included because standing dead trees provide quality nesting habitat for many cavity nesting birds (McClelland and Frissell 1975), and because they also support different insects than do live trees which could impact bark foraging species (Anderson 1960).

While conducting field work, we noted that both the local and landscape-level features varied by county. At the local scale, these differences probably reflected contrasting management strategies and effort. At broad scales these differences may reflect differences in patterns of land use. We therefore used multivariate analysis of variance to compare differences in environmental variables among counties, with a separate analysis conducted for each scale. If the overall test was significant, differences among individual variables were subsequently evaluated.

Next, we tested for interannual differences in bird abundance using a repeated-measures analysis of variance with year as the repeated measure and county as the main effect. Results revealed no interannual effects ($p = 0.16$), or year-by-county interactions ($p = 0.29$). We therefore pooled abundance data across years. Relative species abundances were calculated as the number of individuals detected at a plot averaged over all visits in both years (Nur et al. 1999). Whereas maximum abundance tends to overestimate true avian abundance and is likely to be biased by the inclusion of non-breeders (e.g. floaters) thus inflating estimates of habitat quality, mean abundance is considered a better predictor of reproductive activity than other point count summary statistics (Betts et al. 2005).

To determine if bird community structure (a single data matrix composed of the relative abundances of all species detected at each study plot) differed among counties, we conducted an analysis of similarity (ANOSIM; Minchin 1987) test using the “anosim” function in the vegan

package (Oksanen et al. 2010) for R for Statistical Computing (R Development Core Team 2008). ANOSIM tests for differences in within-group versus among-group community dissimilarity and produces an estimated p-value based on 10,000 Monte Carlo simulations (Clarke 1993). We used the Bray-Curtis distance as a measure of ecological dissimilarity based on its ability to identify ecological gradients (Faith et al. 1987) and because it is less sensitive to differences among rare species. We also conducted a Mantel test (Mantel 1967) in PC-ORD version 6 (McCune and Mefford 2011) to test whether plots that were closer together geographically were more likely to have similar bird communities. Bray-Curtis distance was again used as a measure of ecological dissimilarity, and a probability value was calculated based on 10,000 Monte Carlo simulations.

We used an unconstrained distance-based ordination technique, nonmetric multidimensional scaling (NMDS; Kruskal 1964), to examine community dissimilarity among forest plots using the function "metaMDS" in the vegan package (Oksanen et al. 2010) for R. NMDS is an iterative procedure that is particularly robust to non-normal data, is less prone to spurious results, and has fewer restrictive assumptions than other multivariate methods (Minchin 1987). NMDS graphically arranges samples in ordination space based on a measure of dissimilarity (Faith et al. 1987); therefore points located close together in ordination space represent plots with similar avian community structure. As in the ANOSIM procedure, we used Bray-Curtis distance as the ecological dissimilarity measure. In NMDS, goodness-of-fit is measured by the stress value, which is used to determine the number of dimensions needed to adequately portray the sample units in ordination space and is indicative of how well the configuration matches the data (Kruskal 1964). To assess how avian community structure was related to environmental variables, we used the vector-fitting procedure "envfit" in the vegan

package for R (Okansen et al. 2010). Vector-fitting maximizes the linear correlation between an explanatory variable and the NMDS axes (Kantvilas and Minchin 1989). For each fitted vector we used 10,000 Monte Carlo simulations to generate an estimated p-value.

In order to examine the distribution of individual species in ordination space, we derived correlations of species abundances with ordination axes using PC-ORD. Correlation coefficients that expressed both the linear (Pearson's *r*) and rank (Kendall's τ) relationships between the species and the ordination scores (McCune and Grace 2002) were calculated for the most abundant species (i.e. n > 20 observations summed over the two years). Kendall's τ values express the rank correlation between the ordination scores and individual variables (McCune and Grace 2002). Typically, ecologically meaningful relationships have a Kendall's τ value > 0.25 (McCune and Mefford 2011). These species correlations and ordinations were compared with those of the environmental vectors to gain a better understanding of species-specific responses to measures of invasive vegetation.

Following Grundel and Pavlovic (2007), we used nonparametric multiplicative regression (NPMR) to examine the relationship between environmental variables and community summary statistics as well as two guild level metrics using HyperNiche version 2.0 (McCune 2009). NPMR has been used in a variety of plant (Cazza et al. 2007, Engelbrecht et al. 2007) and animal studies (Grundel and Pavlovic 2007, Miller et al. 2007). NPMR is particularly advantageous because it models nonlinear relationships, automatically considers potential interactions among environmental variables, and combines the effects of explanatory variables multiplicatively as opposed to additively (McCune 2009). Additionally, it produced models that are more parsimonious and fit better than other methods (McCune 2009). NPMR uses the data to specify model form with a local multiplicative smoothing function and a leave-one-out cross-validation,

unlike traditional methods that adopt a global model to determine the value of coefficients with a mathematical equation (McCune 2006). We used a local mean estimator and Gaussian kernel weighting function in a step-wise procedure, wherein data points closer to the target point in environmental space are given greater weight. Statistical tolerances are the standard deviation of the Gaussian weighting function, and have a ready ecological interpretation. We assessed model quality and fit with a cross-validated R^2 (xR^2), and conducted a sensitivity analysis to assess the relative importance of particular predictors within a selected model (McCune 2006). We examined response curves to understand how the community measures changed in response to any measures of invasion selected in the "best" model (e.g. the model with the highest xR^2).

We calculated two community summary statistics that served as response variables: species richness (S), and conservation value. Maintaining species richness is a common goal of conservation management, yet this metric does not place greater value on threatened species or the most important ecological relationships in an area (Fleishman et al. 2006). Conservation value was calculated using a categorical ranking algorithm recommended by Nuttle et al. (2003), in which the relative abundances of species are weighted by species-specific Partners in Flight (PIF) ranks (Beissinger et al. 2000). The conservation value of a particular study plot therefore equaled the sum of these weighted abundances. Lastly, we also modeled the abundance of shrub nesters and aerial insectivores because we thought that these two guilds were the most likely to be influenced by exotic shrub invasions.

In addition to modeling these metrics, we also modeled presence-absence data for six bird species to estimate their likelihood of occurrence using local logistic-NPMR (McCune 2009). We selected species based on two criteria: (1) the species had to have a PIF rank of three or four (corresponding to "moderate" or "high" conservation concern, respectively [Nuttle et al. 2003]),

and (2) the species had to be present in 10-70% of the plots. We used a sub-set of the environmental variables based on *a priori* hypotheses regarding factors that might impact the distribution of each species. Model fit was assessed with the $\log_{10}$ of the likelihood ratio (logB; Pawitan 2001). We then created contour graphs of the best models to gain a better understanding of how these birds responded to the environmental variables. A major strength of the NPMR contour graphs is that they explicitly depict the range over which sufficient data are available to make predictions. See McCune (2009) for a more detailed explanation of NPMR.

Results

Environmental variables

While native brambles (*Rubus* spp.) and hawthorns (*Crataegus* spp.) were encountered in low numbers at a few plots, there was an overall lack of native understory vegetation throughout the sampled forest fragments. A gradient of invasive vegetation however, did exist across the sampled plots (Fig. 2). Wide ranges of all three direct measures of invasion, invasive shrub cover (Fig. 2a), invasive stem density (Fig. 2b), and the percentage of trees that were buckthorn (Fig. 2c) were observed. There were significant differences among counties in terms of both local habitat variables (Wilks' lambda = 0.322; $F = 2.03$; df = 24, 102.11; $p = 0.008$) and landscape measures (Wilks' lambda = 0.125; $F = 6.33$; df = 18, 105.14; $p < 0.001$). All landscape variables differed significantly among counties, as did two local variables: invasive shrub cover and bare ground cover (Table 2). DuPage County had the highest invasive shrub stem density and cover, as well as the highest percentage of buckthorn trees, whereas Lake County had the lowest values for these three features. Bare ground cover was significantly higher in Cook County than in McHenry and DuPage counties. Forest fragments in McHenry County were the smallest and

were surrounded by less forest and urban cover compared to the other counties, which is a result of these fragments being surrounded by relatively more agriculture. McHenry County also had the lowest tree density, and the highest percentage of trees that were oak. Cook County had significantly larger forest fragments than the other three counties, which makes sense because the Forest Preserve District of Cook County owns approximately 27,520 ha (Forest Preserve District of Cook County 2011), more than and other county in this study. Lastly, Cook County was generally the most urbanized, as it had the highest values for both percent urban cover and building density.

Bird community responses

We observed 1,962 individual birds representing 57 songbird species that met our criteria for inclusion in data analyses during the two years of the study. The most common species were the American robin (16.31 % of all observations), red-eyed vireo (*Vireo olivaceus*; 7.64 %), and northern cardinal (*Cardinalis cardinalis*; 7.39%).

Bird community structure differed significantly among counties ($R = 0.16$, $p < 0.01$) and the Mantel test indicated that our study area could be considered statistically independent because there was no significant spatial autocorrelation in bird community structure (Mantel $r = -0.08$, $p = 0.11$). NMDS reached a convergent three-dimensional solution with a stress of 18.61% (Kruskal 1964). We chose to display axes one and two because they had the highest correlations between ordination distances and distances in the original three-dimensional space (Fig. 3). The bird communities in McHenry County were distinct from those in Lake County, and the bird communities in DuPage and Cook counties overlapped substantially in ordination space. These results also hold true for the other axes combinations.

At the local scale, litter cover was the variable most strongly correlated with the arrangement of study plots in ordination space ($r^2 = 0.330$, $p < 0.001$), followed by tree density ($r^2 = 0.257$, $p < 0.001$) and the percentage of trees that were oak ($r^2 = 0.237$, $p = 0.003$; Fig. 3). The vectors for tree density and percentage of trees that were oak were approximately the same length and pointed in almost completely opposite directions since they had a strong negative correlation (r = -0.50; Fig. 3). Overall, the three direct measures of invasive vegetation had similar vector lengths and directions, but they were weakly correlated with avian community structure (invasive shrub cover, $r^2 = 0.113$, $p = 0.084$; invasive stem density, $r^2 = 0.109$, $p = 0.083$; percentage of trees that were buckthorn, $r^2 = 0.066$, $p = 0.232$.). The vectors of the two indirect measures of invasion, tree density and bare ground cover ($r^2 = 0.191$, $p = 0.010$) pointed in similar directions in ordination space (Fig. 3).

At the landscape scale, distance to the nearest edge was the variable most strongly correlated with the arrangement of study plots in ordination space ($r^2 = 0.322$, $p < 0.001$), followed by measures of urbanization, urban land cover ($r^2 = 0.196$, $p = 0.009$) and building density ($r^2 = 0.104$, $p = 0.092$; Fig. 3). All three of these variables pointed in the same direction, away from the plots in McHenry County (Fig. 3). These variables were all positively correlated, and reached their lowest values within McHenry County and their highest values within Cook County (Table 2). Surprisingly, forest area had the weakest correlation with the arrangement of study plots in ordination space ($r^2 = 0.015$, $p = 0.729$; Fig. 3).

All of the "best" NPMR community and guild models contained either a direct measure (percentage of trees that are buckthorn or invasive stem density) or indirect measure (tree density) of invasion (Table 3). Sensitivities indicated that tree density was the most important predictor for species richness. Response curves revealed that species richness decreased as tree

density increased. Conservation value was most sensitive to distance from the nearest edge of the forest fragment and response curves revealed that it generally declined as the percentage of buckthorn trees increased. The steepest decline in conservation value occurred when 60-80% of the trees were buckthorn, indicating a potential threshold. The best shrub nesting guild NPMR model had a relatively high xR^2 value, and included both a direct and indirect measure of invasion. The abundance of shrub nesters was most sensitive to tree density, and the response curve revealed a sharp decline in the number of shrub nesters with an increase in tree density. Response curves also revealed that aerial insectivores reached their lowest abundances in areas with high proportions of buckthorn trees.

Individual species responses

Correlation coefficients were calculated for all of the environmental variables (Appendix A) and the distribution of twenty different bird species with the three NMDS axes (Appendix B). While some birds showed no strong relationships with any of the axes (i.e. the cedar waxwing), many species did. The American robin for example, had a strong positive relationship with axis one (r = 0.540), as well as a strong negative relationship with axis two (r = -0.566). These correlations tightly correspond to the litter cover vector (Fig. 3). Increases in robin abundances therefore follow increases in litter cover in ordination space. Other species that showed clear responses to environmental vectors in ordination space include: the red-eyed vireo with tree density, and the indigo bunting (*Passerina cyanea*) and common yellowthroat (*Geothlypis trichas*) with the percentage of trees that were oak and percent agriculture cover. Positive species correlations with axis two indicated positive associations with invasion, as the measures of invasion (both direct and indirect) were the only environmental variables that had an $r > 0.20$ with this axis.

Intuitively, the shrub-nesting northern cardinal, showed a strong positive response to all three invasive vegetation vectors in ordination space. While three additional species, the blue-gray gnatcatcher (*Polioptila caerulea)*, house wren (*Troglodytes aedon*), and gray catbird (*Dumetella carolinensis*) demonstrated positive albeit weaker responses to invasion, most species showed a negative response or no response at all.

Six species met our criteria for further NPMR analysis. All of the best logistic-NPMR species models had two variables out of a possible 11-13 total (Table 4). Direct measures of invasive vegetation were included in half of the models, and the percentage of trees that were buckthorn was the most frequently selected environmental variable. While the wood thrush was more likely to occur in areas with moderate to high levels of invasive vegetation, both the great-crested flycatcher (*Myiarchus crinitus*) and the hooded warbler (*Wilsonia citrine*) were less likely to occur in areas with a high proportion of buckthorn trees (Fig. 4). Landscape variables were selected in the best models for three species.

The likelihood of occurrence for most species was at a maximum near the extremes of one or both environmental gradients (Fig. 4). For example, the blue-gray gnatcatcher reached its' highest probability of occurrence in areas with a relatively high percentage of oak trees and at the lower observed values of urban cover. Conversely, the wood thrush, showed a hump-shaped response to invasive stem density, yet reached its highest probability of occurrence in areas with a relatively high proportion of buckthorn trees. For a few species, the highest projected probabilities of occurrence only occupied a small section of the ecological space defined by the environmental gradients. For example, the highest probability of occurrence of the hooded warbler occupied a small section of the space defined by building density and the percentage of trees that were buckthorn. Hooded warblers were more sensitive to building density than to the

percentage of trees that were buckthorn, so the zone of highest probability of occurrence for the hooded warbler was subsequently more restricted along the building density gradient.

Discussion

We found that whereas the direct measures of invasive vegetation were weakly correlated with avian community structure, they were selected as important variables in predicting community and guild metrics as well as the occurrence of species of conservation concern in the region. For example, both the hooded warbler and the great-crested flycatcher were more likely to occur in areas with a low percentage of buckthorn trees. These species are aerial insectivores and their foraging ability is likely inhibited by the dense understory and overstory structure created by buckthorn invasions. Relatively open forest canopies have been shown to support greater populations of aerial insectivores (Kotliar et al. 2002) and the eastern wood-pewee (*Contopus virens*; a common canopy species) has been found in lower densities in sites invaded by honeysuckle than in sites with native shrub understories (McCusker et al. 2010). Other studies have found that management aimed at reducing understory shrub density can lead to greater abundances of eastern wood-pewees (Wilson et al. 1995), as well as other bird species that prefer to forage in more open habitats (Brawn 2006). Another potential explanation for this observed trend is that buckthorn does not provide ideal food resources for these insectivores since invasive exotic plants generally support less abundant and species rich insect communities than do native plant (Wu et al. 2009, Litt and Steidl 2010). Another factor to consider is that great-crested flycatchers prefer large cavities because they build rather bulky nests (Bent 1942), so perhaps small buckthorn trees do not provide suitable nesting sites for this species. All of these reasons

may have contributed to the finding that conservation value decreased with increased buckthorn tree dominance.

Contrary to these negative responses, one species of great conservation concern, the wood thrush was more likely to occur in heavily invaded areas and the abundances of several common shrub-nesting species were positively associated with invasive shrubs. Overall, our results are consistent with our original expectation that shrub-nesting species would prefer invaded forests where nesting substrate is actually present. Other studies have demonstrated that abundances of understory species like the northern cardinal are positively associated with invasive shrubs (Leston and Rodewald 2006, McCusker et al. 2010). The wood thrush generally prefers moist shady areas with a moderate subcanopy and shrub density (Evans et al. 2001); however this species has experienced large population declines in recent decades (Sauer et al. 1996). Some studies have found that if wood thrushes nest in dense understories they may be more vulnerable to predation (Newell and Kostalos 2007), and that both honeysuckle and buckthorn may serve as ecological traps for this, as well as other shrub-nesting species (Schmidt and Whelan 1999).

Our two indirect measures of invasion, bare ground cover and tree density, were more strongly correlated with avian community structure than the direct measures of invasion. Additionally, species richness decreased as tree density increased, which might be due to a decrease in the number of shrub-besting species. Increased tree densities likely also have a negative effect on avian species that prefer more open habitat. Similar to our findings, other studies have reported lower avian species richness and density in areas with high densities of small trees (James and Warner 1982). Bare ground cover was associated with an increase in buckthorn tree dominance, yet it remains unclear whether it influenced the habitat selection of

ground foraging birds by increasing their access to soil invertebrates (Perkins et al. 2000). Data from a study conducted on a sub-set of these plots in 2010 however, suggest that invasive earthworm biomass shows a strong positive correlation with bare ground cover and is a strong predictor of American robin distributions (Cleeton and Umek, *unpublished data*).

An unexpected outcome of this research was that study plots grouped together in ordination space by county, and not because the sites were in closer proximity to one another. Essentially, county served as an excellent surrogate variable because it captured a lot of the variation in the environmental variables, particularly those at landscape scales. Also, some local habitat variables still showed differences among counties even though we selected for a gradient of invasion within each county. In other words, a study plot that was considered to be "degraded" in one county could be quite different in terms of invasive vegetation than a different county. This finding is probably a result of the fact that the majority of the plots were originally selected by asking land managers to group plots into distinct categories (see Methods: site selection). These decisions were clearly subjective and the views of the land managers concerning what constituted a "degraded" or a "recently restored" plot differed by county. We suspect that the amount of money a county forest preserve district has, influences the management efforts occurring within its preserves. Lake County for example, has the highest median household income of any county in Illinois (U.S. Census Bureau 2009), and it is therefore not surprising that this county had the least invaded study plots. This Forest Preserve District may potentially have the most money to spend on restoration efforts, or perhaps this is a result of Lake County just having less total land to manage.

Another finding that emerged from this study was that several local and landscape-scale variables were strongly correlated with bird community structure, and were selected as the best

variables for predicting the occurrence of species of conservation concern. At the local scale both litter cover and the percentage of trees that were oak were salient variables. For example, both the northern flicker (*Colaptes auratus*) and the American redstart (*Setophaga ruticilla*) responded positively to an increase in the dominance of oak trees. Oaks tended to be the largest trees in our study area, and large trees can have a positive effect on avian diversity. Additionally, oak trees have been recognized as keystone structures that provide crucial habitat resources such as acorns for wildlife, particularly in urban areas (Stagoll et al. 2012). Oak trees tend to support greater insect species richness and abundance than other tree species in temperate forests (Summerville et al. 2003), and they can therefore provide abundant food sources for insectivorous birds like the American redstart. Northern flickers have previously been found to be more abundant in oak than in maple stands (Rodewald and Abrams 2002). The great-crested flycatcher was more likely to occur in areas with high litter cover perhaps because this species is a secondary cavity nester that fills natural cavities with dead leaves, among other nesting material (Taylor and Kershner 1991). In our study, litter cover was a function of two factors: buckthorn invasion and time since fire. Generally, there was less litter in areas that had been recently burned, or that were heavily invaded with buckthorn which produces a large amount of nitrogen-rich organic matter that decomposes relatively quickly compared to the litter of trees native to Illinois (Heneghan et al. 2002).

At the landscape scale three variables were highly correlated with bird community structure: distance to nearest edge, and the two measures of urbanization (percent urban land cover and the building density in the surrounding landscape). Proximity to edges can play a major role in structuring avian communities (Baker et al. 2002), as can the degree of urbanization surrounding forest fragments (Friesen et al. 1995). For example, the abundance and

diversity of forest-dwelling neotropical migrants can decrease in both abundance and diversity as the level of residential development increases, regardless of fragment size (Friesen et al. 1995). In our study the hooded warbler probably reached its highest likelihood of occurrence in forests surrounded by lower building densities because it is a ground nesting, insectivorous, neotropical migrant, features that typify urban avoider species (Blair 2001). This finding is congruent with a study by Smith and Schaefer (1992) who reported that hooded warblers reached higher densities in a non-urban forest than in an urban forest fragment.

Conclusions

Considerable resources are spent on eradication programs as part of ecological restoration efforts (Pimentel et al. 2000), yet the consequences of these actions are not always fully understood. Our results contribute to the growing body of research on animal utilization of invaded habitats. Specifically, we found that species richness and conservation value showed negative responses to buckthorn tree dominance within an urban landscape. When developing management plans however, species-specific responses to invasive shrubs should be taken into consideration, as certain species may actually benefit from these invasions.

Our findings indicate that management strategies aimed solely at the removal of invasive vegetation may improve the foraging ability of aerial insectivores. Complete clearance of the invasive understory however, would likely negatively impact shrub-nesting species, as little or no other nesting substrate would be available. Nevertheless, it has been demonstrated that these invasive shrubs can act as ecological traps for nesting songbirds (Schmidt and Whelan 1999, Borgmann and Rodewald 2004). We therefore recommend restoring the native shrub understory in addition to invasive shrub removal. Unfortunately, research has demonstrated that this may

not be feasible however, because native vegetation is not always able to persist in urban soils that had been invaded by exotic plants (Pavao-Zuckerman 2008). Therefore, in order to effectively restore these urban woodlands to pre-settlement conditions (a common habitat restoration goal), soil amelioration and alternative management strategies may need to be taken into consideration (Pavao-Zuckerman 2008).

It is important to note that while higher density is not always associated with greater fitness (van Horne 1983), generally, bird surveys can act as an indicator of environmental conditions and habitat quality, and they are also an accepted method for informing management decisions (Bock and Jones 2004). More mechanistic studies that quantify breeding success in invasive shrubs, or examine potential bottom-up effects are clearly needed. The only study that has compared predation of nests in buckthorn to that of nests in native shrubs took place in an arboretum and an adjacent forest preserve in the Chicago suburbs (Schmidt and Whelan 1999). These researches likely conducted their study at the arboretum because that may have been one of the only areas where native shrubs were common. Studies that examine nest success along a gradient of buckthorn invasion in more realistic and natural areas are clearly needed. Additionally, only one investigation has surveyed insects associated with European buckthorn (Gassmann et al. 2008), and to our knowledge no studies have compared this insect community with that of a forest with a native understory in the same region. Lastly, we suggest that an experimental approach be taken to examine how bird communities respond to different management practices and restoration treatments over time.

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References

Anderson, R. 1960. Forest and shade tree entomology. John Wiley and Sons, New York.

Apfelbaum, S. and A. Haney. 1991. Management of degraded oak savanna remnants in the upper Midwest: preliminary results from three years of study. Pages 81-89 in G.V. Burger, J.E. Ebinger, and G.S. Wilhelm, eds. Proceedings of the Oak Woods Management Symposium. Eastern Illinois University, Charleston.

Baker, J., K. French, and R. J. Whelan. 2002. The edge effect an ecotonal species: bird communities across a natural edge in southeastern Australia. Ecology 83: 3048-3059.

Bartuszevige, A. M., and D. L. Gorchov. 2006. Avian seed dispersal of an invasive shrub. Biological Invasions 8: 1013-1022.

Beissinger, S. R., J. M. Reed, J. M. Wunderle, Jr., S. K. Robinson, and D. M. Finch. 2000. Report of the AOU Conservation Committee on the Partners in Flight species prioritization plan. Auk 117:549-561.

Bent, A. C. 1942. Life histories of North American flycatchers, larks, swallows and their allies. Bulletin of the United States National Museum 179.

Betts, M. G., N. P. Simon, and J. J. Nocera. 2005. Point count summary differentially predict reproductive activity in bird-habitat relationship studies. Journal of Ornithology 146: 151-159.

Bibby, C. J., N. D. Burgess, D. A. Hill, and S. H. Mustoe. 2000. Bird Census Techniques. Elsevier Ltd., London, U.K.

Blair, R. B. 2001. Birds and butterflies along urban gradients in two ecoregions of the U.S. Pages 33-56 in Lockwood, J. L., and M. L. McKinney, eds. Biotic Homogenization. Norwell (MA): Kluewer.

Bock, C. E., and Z. F. Jones. 2004. Avian habitat evaluation: should counting birds count? Frontiers in Ecology and the Environment 2: 403-410.

Borgmann, K. L., and A. D. Rodewald. 2004. Nest predation in an urbanizing landscape: the role of exotic shrubs. Ecological Applications 14:1757-1765.

Borgmann, K. L., and A. D. Rodewald. 2005. Forest restoration in urbanizing landscapes: interactions between land uses and exotic shrubs. Restoration Ecology 13: 334-340.

Brawn, J. D. 2006. Effects of restoring oak savannas on bird communities and populations. Conservation Biology 20: 460-469.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Cornwall.

Casazza, G., E. Zappa, M. G. Mariotti, F. Médail and L. Minuto. 2007. Ecological and historical factors affecting distribution pattern and richness of endemic plant species: the case of the Maritime and Ligurian Alps hotspot. Diversity and Distributions 14: 47-58.

Clarke, K. R. 1993. Nonparametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117-143.

Cody, M. L. 1985. An introduction to habitat selection in birds. In: Cody, N. L. (Ed.), Habitat Selection in Birds. Academic Press, Orlando, pp. 4-56.

Davis, M.A., M.K. Chew, R.J. Hobbs, A.E. Lugo, J.J. Ewel, G.J. Vermeij, J.H. Brown, M.L. Rosenzweig, M.R. Gardener, S.P. Carroll, K. Thompson, S.T.A. Pickett, J.C. Stromberg, P.D. Tredici, K.N. Suding, J.G. Ehrenfeld, J. Philip Grime, J. Mascaro, and J.C. Briggs. 2011. Don't judge species on their origins. Nature 474: 153-154.

Ellis, L.M. 1995. Bird use of saltcedar and cottonwood vegetation in the Middle Rio Grande Valley of New Mexico, U.S.A. Journal of Arid Environments 30: 339-349.

Engelbrecht, B. M. J., L. S. Comita, R. Condit, S. P. Hubbell, T. Kursar, and M. Tyree. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. Nature 447: 80-82.

Evans, Melissa, Elizabeth Gow, R. R. Roth, M. S. Johnson and T. J. Underwood. 2011. Wood Thrush (*Hylocichla mustelina*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/246

Faith, D. P., P. R. Minchin, and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69: 57-68.

Flieshman, E., R. F. Noss, and B. R. Noon. 2006. Utility and limitations of species richness metrics for conservation planning. Ecological Indicators 6: 543-553.

Forest Preserve District of Cook County. 2011. Preliminary Capital Improvement Plan 2012-2016. http://fpdcc.com/preliminary-capital-improvement-plan-2012-2016-posted

Friesen, L. E., P. F. J. Eagles, and R. J. Mackay. 1995. Effects of residential development on forest-dwelling neotropical migrant songbirds. Conservation Biology 9: 1408-1414.

Frost, J.S., and L.A. Powell. 2011. Cedar infestation impacts avian communities along the Niobrara River Valley, Nebraska. Restoration Ecology 19: 529-536.

Gassman, A., I. Tosevski, and L. Skinner. 2008. Use of native range surveys to determine the potential host range of arthropod herbivores for biological control of two related weed species, *Rhamnus cathartica* and *Frangula alnus*. Biological Control 45: 11-20.

Germaine, S.S., S.S. Rosenstock, R.E. Schweinsburg, and W.S. Richardson. 1998. Relationships among breeding birds, habitat, and residential development in greater Tucson, Arizona. Ecological Applications 8: 680-691.

Godwin, H. 1943. Biological flora of the British Isles: *Rhamnaceae*. Journal of Ecology 31: 66-92.

Grundel, R., and N. B. Pavlovic. 2007. Response of bird species densities to habitat structure and fire history along a Midwestern open–forest Gradient. The Condor 109: 734–749.

Haskell, D. G. 2000. Effects of forest roads on macroinvertebrate soil fauna of the southern Appalachian Mountains. Conservation Biology 14: 57-63.

Heimpel, G. E., L. E. Frelich, D. A. Landis, K. R. Hopper, K. A. Hoelmer, Z. Sezen, M. K. Asplen, K. Wu. 2010. European buckthorn and Asian soybean aphid as components of an extensive invasional meltdown in North America. Biological Invasions 12: 2913-2931.

Heneghan, L., C. Clay, and C. Brundage. 2002. Rapid decomposition of buckthorn litter may change soil nutrient levels. Ecological Restoration 20: 108-111.

Hobbs, R. J. 2000. Land-use changes and invasions. Pages 55-64 in H. A. Mooney and R. J. Hobbs, eds. Invasive species in a changing world. Island Press, Washington, D. C.

Hunter, W.C., R.D. Ohmart, and B.W. Anderson. 1988. Use of exotic salt cedar (*Tamarix chinensis*) by birds in arid riparian systems. The Condor 90: 113-123.

van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47: 893-901.

James, F. C., and N. O. Warner. 1982. Relationships between temperate bird communities and vegetation structure. Ecology 63: 159-171.

Kantvilas, G., and P. R. Minchin. 1989. An analysis of epiphytic lichen communities in Tasmanian cool temperate rainforest. Vegetatio 84: 99-102.

Knight, K. S., J. S. Kurylo, A. G. Endress, J. R. Stewart, and P. B. Reich. 2007. Ecology and ecosystem impacts of common buckthorn (*Rhamnus catartica*): a review. Biological Invasions 9: 925-937.

Kotliar, N. B., S. J. Hejl, R. L. Hutto, V. A. Saab, C. P. Melcher, and M. McFadzen. 2002. Effects of fire and postfire salvage logging on avian communities in conifer-dominated forest of the western United States. Studies in Avian Biology 25: 49-64.

Kruskal, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. Psychometrika 29: 115-129.

Laurance, W. F., and E. Yensen. 1991. Predicting the impacts of edge effects in fragmented habitats. Biological Conservation 55: 77-92.

Leston, L., and A. D. Rodewald. 2006. Are urban forests ecological traps for understory birds? An examination using Northern cardinals. Biological Conservation 131: 566-574.

Litt, A. R., and R. J. Steidl. 2010. Insect assemblages change along a gradient of invasion by a nonnative grass. Biological Invasions 12: 3449-3463.

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10: 689-710.

Mantel, N. 1967. The detection of disease clustering and generalized regression approach. Cancer Research 27: 209-220.

Martin, T. E., C. R. Paine, C. J. Conway, W. M. Hochachka, P. Allen, and W. Jenkins. 1997. BBIRD field protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula.

Matlack, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. Biological Conservation 66: 185-194.

Mattsson, B. J., and G. J. Niemi. 2006. Factors influencing predation on Ovenbird (*Seiurus aurocapilla*) nests in northern hardwoods: interactions across spatial scales. Auk 123: 82-96.

McClelland, B. R., and S. S. Frissell. 1975. Identifying forest snags useful for hole-nesting birds. Journal of Forestry 73: 414-417.

McCune, B. 2006. Non-parametric habitat models with automatic interactions. Journal of Vegetation Science 17: 819-830.

McCune, B. 2009. Nonparametric Multiplicative Regression for Habitat Modeling. (http://www.pcord.com/NPMRintro.pdf).

McCune, B., and J. B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon.

McCune, B. and M. J. Mefford. 2011. PC-ORD. Multivariate Analysis of Ecological Data. Version 6. MjM Software, Gleneden Beach, Oregon.

McCusker, C. E., M. P. Ward, and J. D. Brawn. 2010. Seasonal responses of avian communities to invasive bush honeysuckles (*Lonicera* spp.). Biological Invasions 12: 2459-2470.

McPherson, E. G., D. J. Nowak, S. Grimmond, R. Grant, and R. A. Rowntree. 1997. Quantifying urban forest structure, function, and value: the Chicago Urban Forest Climate Project. Urban Ecosystems 1: 49-61.

Meister, S. 2006. Response of forest songbird abundance to invasive plant management. Forest Preserve District of DuPage County Report.

Miller, S. W., D. Wooster, and J. Li. 2007. Resistance and resilience of macroinvertebrates to irrigation water withdrawals. Freshwater Biology 52: 2494-2510.

Minchin, P. R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio 69: 89-107.

Newell, F. L., and M. S. Kostalos. 2007. Wood thrush nests in dense understory may be vulnerable to predators. The Wilson Journal of Ornithology 119: 693-702.

Nur, N., S. L. Jones, and G. R. Geupel. 1999. Statistical guide to data analysis of avian monitoring programs. USDI Fish and Wildlife Service Biological Technical Publication BTP-R6001–1999, Washington, D. C.

Nuttle, T., A. Leidolf, and L. W. Burder, Jr. 2003. Assessing conservation value of bird communities with Partners In Flight-based ranks. Auk 120: 541-549.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2010. Vegan: Community Ecology Package. R. package version 1.17-2. (http://CRAN.R-project.org/package=vegan)

Pavao-Zuckerman, M.A. 2008. The nature of urban soils and their role in ecological restoration in cities. Restoration Ecology 16: 642-649.

Pawitan, Y. 2001. In All Likelihood. Statistical Modeling and Inference Using Likelihood. Clarendon Press, Oxford.

Perkins, A. J., M. J. Whittingham, R. B. Bradbury, J.D. Wilson, A.J. Morris, and P. R. Barnett. 2000. Habitat characteristics affecting use of lowland agricultural grasslands by birds in winter. Biological Conservation 95: 279-294.

Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. Bioscience 50: 53-65.

R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austra. (http://www.R-project.org)

Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. Report No. PSW-GTR-144, USDA Forest Service, Albany, CA.

Reichard, S. H., L. Chalker-Scott, and S. Buchanan. 2001. Interactions among non-natives plants and birds. In: Marzluff, J., R. Bowman, and R. Donnelly (eds) Avian ecology and conservation in an urbanizing world. Norwell, Massachusetts, pp 179-223.

Rodewald, A. D., and M. D. Abrams. 2002. Floristics and avian community structure: implications for regional changes in eastern forest composition. Forest Science: 48: 267-272.

Rodewald, A. D., D. P. Shustack, and L. E. Hitchcock. 2010. Exotic shrubs as ephemeral ecological traps for nesting birds. Biological Invasions 12: 33-39.

Sauer, J. R., S. Schwartz, B. G. Peterjohn, and J. E. Hines. 1996. North American breeding bird survey results and analysis; Version 96.4. Patuxent Wildlife Research Center, Laurel, Maryland.

Schmidt, K. A., and C. J. Whelan. 1999. Effects of exotic *Lonicera* and *Rhamnus* on songbird nest predation. Conservation Biology 13: 1502-1506.

Smith, D. A., and S. D. Gehrt. 2010. Bat response to woodland restoration within urban forest fragments. Restoration Ecology 18: 914-923.

Smith, R. J., and J. M. Schaefer. 1992. Avian characteristics of an urban riparian strip corridor. The Wilson Bulletin 104: 732-738.

Stagoll, K., D. B. Lindenmayer, E. Knight, J. Fischer, and A. D. Manning. 2012. Large trees are keystone structures in urban parks. Conservation Letters 5: 1-8.

Sullivan, J. 2011. An Atlas of Biodiversity. Chicago Wilderness. Chicago, IL.

Summerville, K. S., T. O. Crist, J. K. Kahn, and J. C. Gering. 2003. Community structure of arboreal caterpillars within and among four tree species of the eastern deciduous forest. Ecological Entomology 28: 747-757.

Taylor, W. K., and M. A. Kershner. 1991. Breeding biology of the Great crested flycatcher in central Florida. Journal of Field Ornithology 62: 28-39

Umek, L. 2009. The Chicago Wilderness Land Management Research Program: 100 Sites for 100 Years. Master Document.

U. S. Census Bureau. State and County QuickFacts, Lake County, Illinois. [online] http://quickfacts.census.gov/qfd/states/17/17097.html

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. The Journal of Wildlife Management 47: 893-901.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. BioScience 48: 607-615.

Wilson, C. W., R. E. Masters, and G. A. Bukenhofer. 1995. Breeding bird response to pine grassland community restoration for red-cockaded woodpeckers. Journal of Wildlife Management 59: 56-67.

Wu, Y., C. Wang, X. Zhang, B. Zhao, L. Jiang, J. Chen, and B. Li. 2009. Effects of saltmarsh invasion by *Spartina alterniflora* on arthropod community structure and diets. Biological Invasions 11: 635–649.

Tables

Table 1. Local and landscape-level variables used as correlates of woodland bird community structure in northeastern Illinois, 2010-2011.

Variable description	Variable code	Mean	Range
Local			
Percent invasive shrub cover	INV_SHRUB	19.79	0-91.33
Invasive shrub stem density (stems per ha)	INV_STEM	5,391.88	0-17,952.64
Percentage of trees that are buckthorn	BUCK_TREE	14.93	0-84.89
Percentage of trees that are oak	OAK_TREE	34.77	0-87.50
Tree density (trees per ha)	TREE_DEN	407.66	59.86-2,062.82
Snag density (snags per ha)	SNAG_DEN	40.06	0-174.50
Percent bare-ground cover	AVG_BG	12.73	2.50-50.63
Percent litter cover	AVG_LITTER	40.91	2.50-87.5
Landscape			
Distance to nearest edge (m)	EDGE_DIST	156.94	54-375
Forest fragment area (ha)	FOREST_AREA	95.50	8-619
Percent agricultural cover (within 1 km)	AG_COV	4.11	0-45.90
Percent forest cover (within 1 km)	FOREST_COV	41.62	11.44-72.28
Percent urban cover (within 1 km)	URBAN_COV	37.41	1.19-88.13
Building density (number of buildings per ha)	BUILD_DEN	1.33	0.01-8.37

Table 2. Values (mean ± 1 SE) for local and landscape variables measured in or around study plots in each county. See Table 1 for explanation of environmental variable codes.

Variable	Cook County (n = 20)	Lake County (n = 11)	DuPage County (n = 10)	McHenry County (n = 5)
Local				
INV_SHRUB	12.4^{a} ± 3.9	7.7^{a} ± 3.1	44.2^{b} ± 12.2	27.4^{ab} ± 16.1
INV_STEM	5,414.4 ± 1,216.7	2,833.0 ± 933.3	7,728.6 ± 2,102.7	6,086.1 ± 1,736.8
BUCK_TREE	12.9 ± 5.2	10.2 ± 6.3	18.5 ± 5.4	14.6 ± 12.0
OAK_TREE	29.3 ± 3.8	37.5 ± 4.4	32.7 ± 10.2	54.9 ± 12.1
TREE_DEN	496.1 ± 88.6	414.15 ± 81.7	371.4 ± 60.9	112.2 ± 18.3
SNAG_DEN	53.9 ± 8.1	38.5 ± 14.6	53.0 ± 12.6	17.4 ± 13.3
AVG_BG	18.59^{a} ± 3.75	12.10^{ab} ± 2.82	6.19^{b} ± 1.80	3.75^{b} ± 1.25
AVG_LITTER	44.50 ± 7.15	42.33 ± 10.06	49.25 ± 9.87	6.75 ± 1.79
Landscape				
EDGE_DIST	210.9^{a} ± 16.6	130.4^{b} ± 16.6	127.2^{bc} ± 20.8	61^{c} ± 3.8
FOREST_AREA	156.6^{a} ± 31.8	63.2^{b} ± 16.6	39.0^{b} ± 5.8	35.4^{b} ± 15.9
AG_COV	0.8^{a} ± 0.4	10.1^{b} ± 5.0	0.2^{a} ± 0.2	11.9^{b} ± 3.9
FOREST_COV	45.4^{a} ± 1.9	40.8^{a} ± 4.5	43.5^{a} ± 5.9	24.7^{b} ± 3.2
URBAN_COV	44.0^{a} ± 3.1	34.6^{a} ± 6.0	42.9^{a} ± 7.8	6.4^{b} ± 1.0
BUILD_DEN	2.1^{a} ± 0.4	0.7^{b} ± 0.1	1.3^{ab} ± 0.5	0.1^{b} ± 0.02

Superscripts within rows indicate significant differences among counties (Fischer's LSD, $p < 0.05$).

Table 3. “Best” nonparametric multiplicative regression (NPMR) model for estimating two community metrics species richness (S), conservation value (CV), as well as the relative abundances of two avian guilds shrub nesters (SHRUB) and aerial insectivores (AERIAL). Models are sorted by descending cross-validated r-squared (xR^2) value within in response variable category, so models at the top of the table have more support than those at the bottom. Direct and indirect measures of invasive vegetation are in bold. K indicates the number of predictor variables. Sensitivities represent the relative importance of particular variables within a given multivariate model. Tolerances are the standard deviation of the Gaussian weighting function, and are in the same units as the environmental variables. See Table 1 for explanation of environmental variable codes.

Response variable	k	Environmental variables	Sensitivities	Tolerances	xR^2
Community					
S	4	**TREE_DEN** and AVG_LITTER and FOREST_AREA and FOREST_COV	0.84, 0.09, 0.04, 0.13	100.64, 1.20, 274.95, 15.21	0.26
CV	2	**BUCK_TREE** and EDGE_DIST	0.20, 1.04	12.73, 16.25	0.25
Guild					
SHRUB	3	**TREE_DEN** and **INV_STEM** and EDGE_DIST	0.86, 0.03, 0.20	100.65, 12566.84, 32.50	0.51
AERIAL	2	**BUCK_TREE** and FOREST_AREA	0.16, 0.17	87.56, 91.65	0.10

Table 4. Logistic-nonparametric multiplicative regression (l-NPMR) model results for estimating the likelihood of occurrence for six bird species of conservation concern. Models are sorted by descending logB, so models at the top of the table have more support than those at the bottom. Predictors that are direct measures of invasive vegetation are in bold. K indicates the number of predictor variables in the "best" model. Sensitivities represent the relative importance of particular variables within a given multivariate model. Tolerances are the standard deviation of the Gaussian weighting function, and are in the same units as the environmental variables. See Table 1 for explanation of environmental variable codes.

Common name	k	Environmental variables	Sensitivities	Tolerances	logB
American redstart	2	OAK_TREE and FOREST_AREA	2.03, 0.34	4.38, 91.65	2.62
Great-crested flycatcher	2	**BUCK_TREE** and AVG_LITTER	0.34, 0.34	12.73, 1.2	2.49
Hooded warbler	2	**BUCK_TREE** and BUILD_DEN	0.13, 1.15	12.73, 0.42	1.25
Northern flicker	2	OAK_TREE and URBAN_COV	0.39, 1.49	21.88, 4.35	0.54
Blue-gray gnatcatcher	2	FOREST_AREA and AG_COV	0.43, 0.07	61.10, 11.47	0.53
Wood thrush	2	**BUCK_TREE** and **INV_STEM**	0.20, 0.61	16.98, 2,692.90	0.21

Figures

Figure 1**.** Black polygons represent the size and locations of the 34 forest fragments within four counties in northeastern Illinois.

Figure 2. Graphs illustrating the invasive vegetation gradient sampled at the 46 study plots in northeastern Illinois. Direct measures of invasive vegetation include: (a) invasive shrub cover, (b) invasive stem density and (c) percentage of trees that are buckthorn.

Figure 3. Nonmetric multidimensional scaling (NMDS) of breeding bird community structure in 46 study plots in northeastern Illinois between 2010 and 2011. Environmental vectors are oriented toward the direction of greatest increase in that variable. The length of an environmental vector is proportional to r^2 and the angle between vectors indicates the correlation between variables. Points are divided among four counties: Cook (white circles), Lake (black circles), DuPage (white triangles), and McHenry (black triangles). See Table 1 for explanation of environmental variable codes.

Figure 4. Estimated likelihood of occurrence for six different bird species as determined by logistic-nonparametric multiplicative regression (l-NPMR) for birds surveyed at 46 plots in northeastern Illinois between 2010 and 2011. The contour graphs illustrate the predicted likelihood of occurrence (indicated by numbers on the graph) as a function of the environmental variable that the species is most sensitive to (x axis), and second most sensitive to (y axis). Lighter shading corresponds to higher occurrence probabilities. White areas in the graphs

indicate locations in the environmental space where predictions were not made due to insufficient data. See Table 1 for explanation of environmental variable codes.

Figure 1.

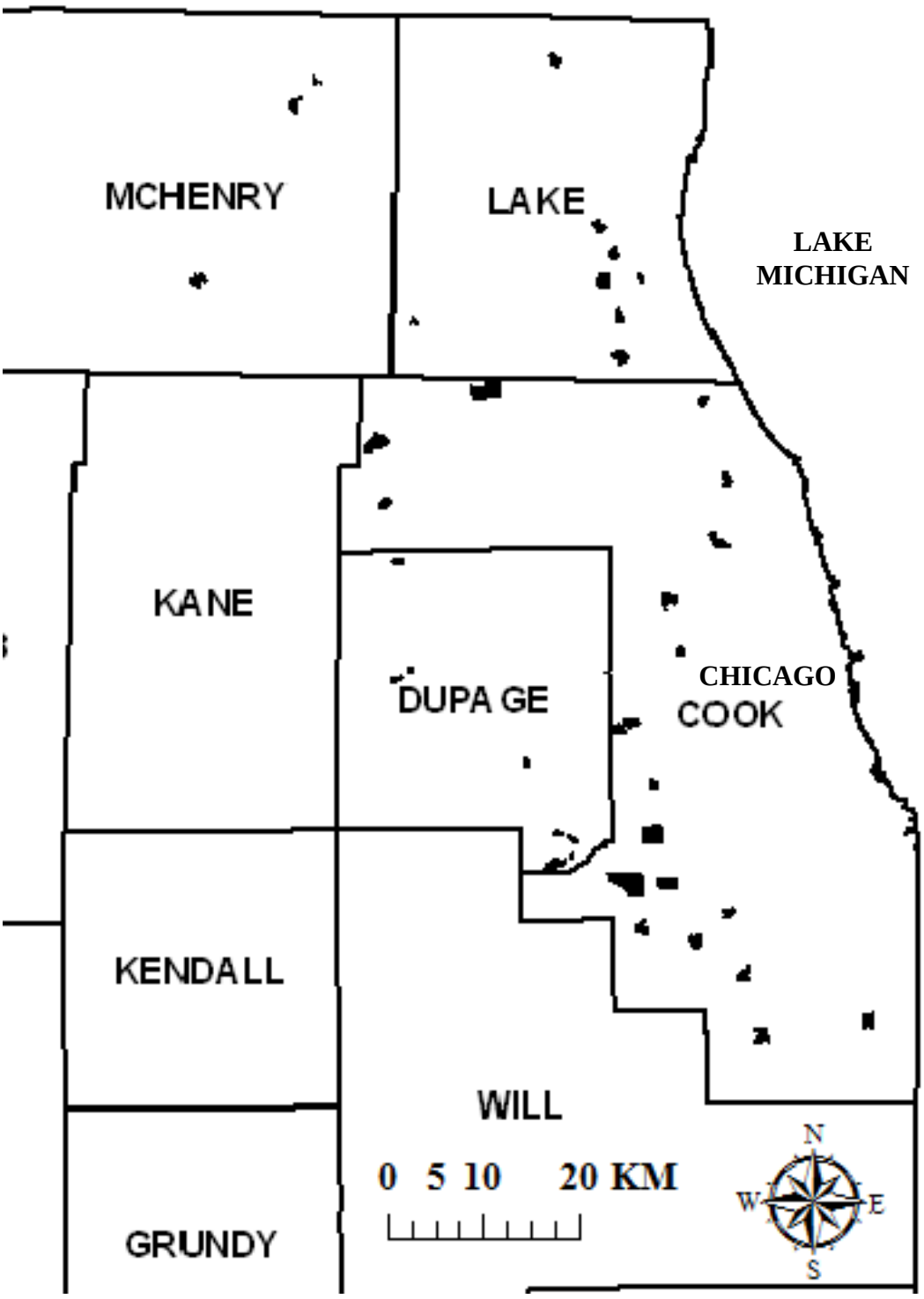
MCHENRY
LAKE
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Figure 2.

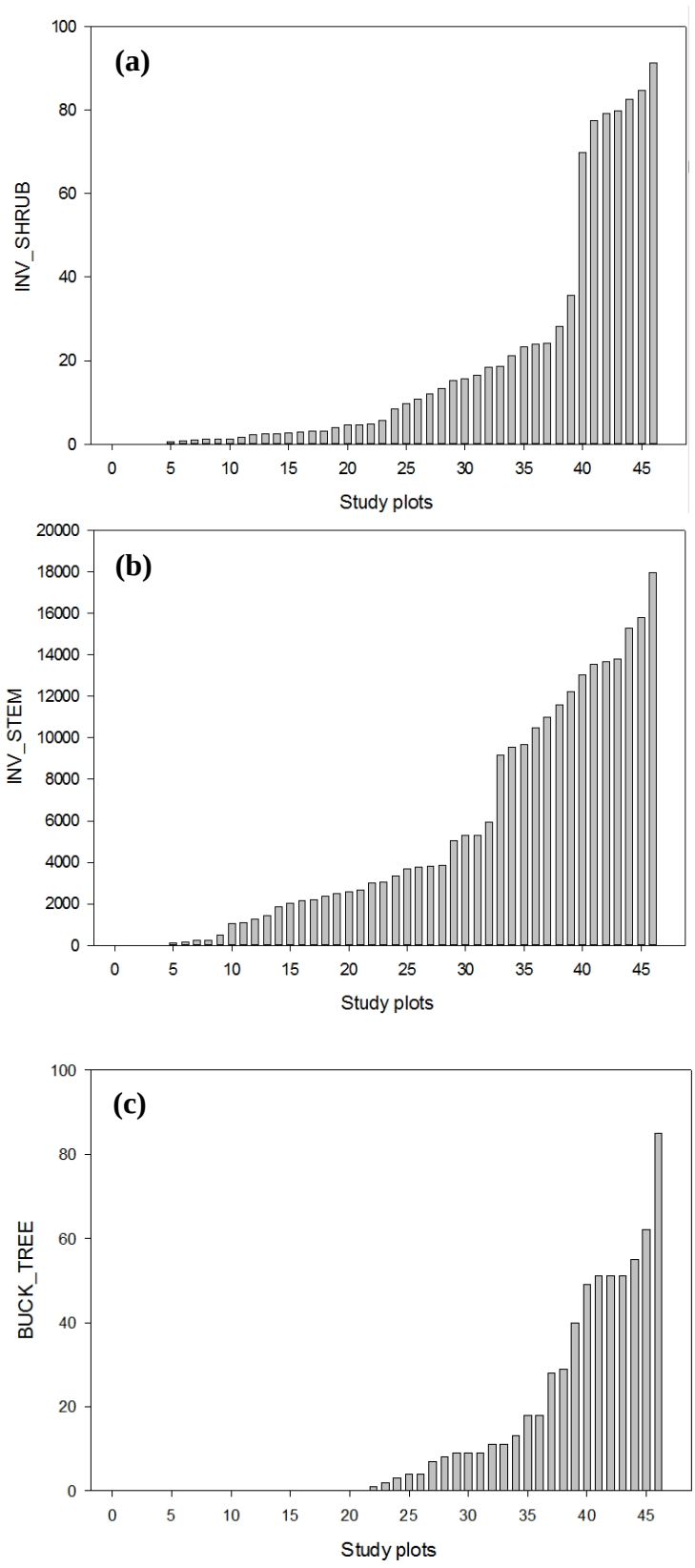

(a)
INV_SHRUB
Study plots
(b)
INV_STEM
Study plots
(c)
BUCK_TREE
Study plots

Figure 3.

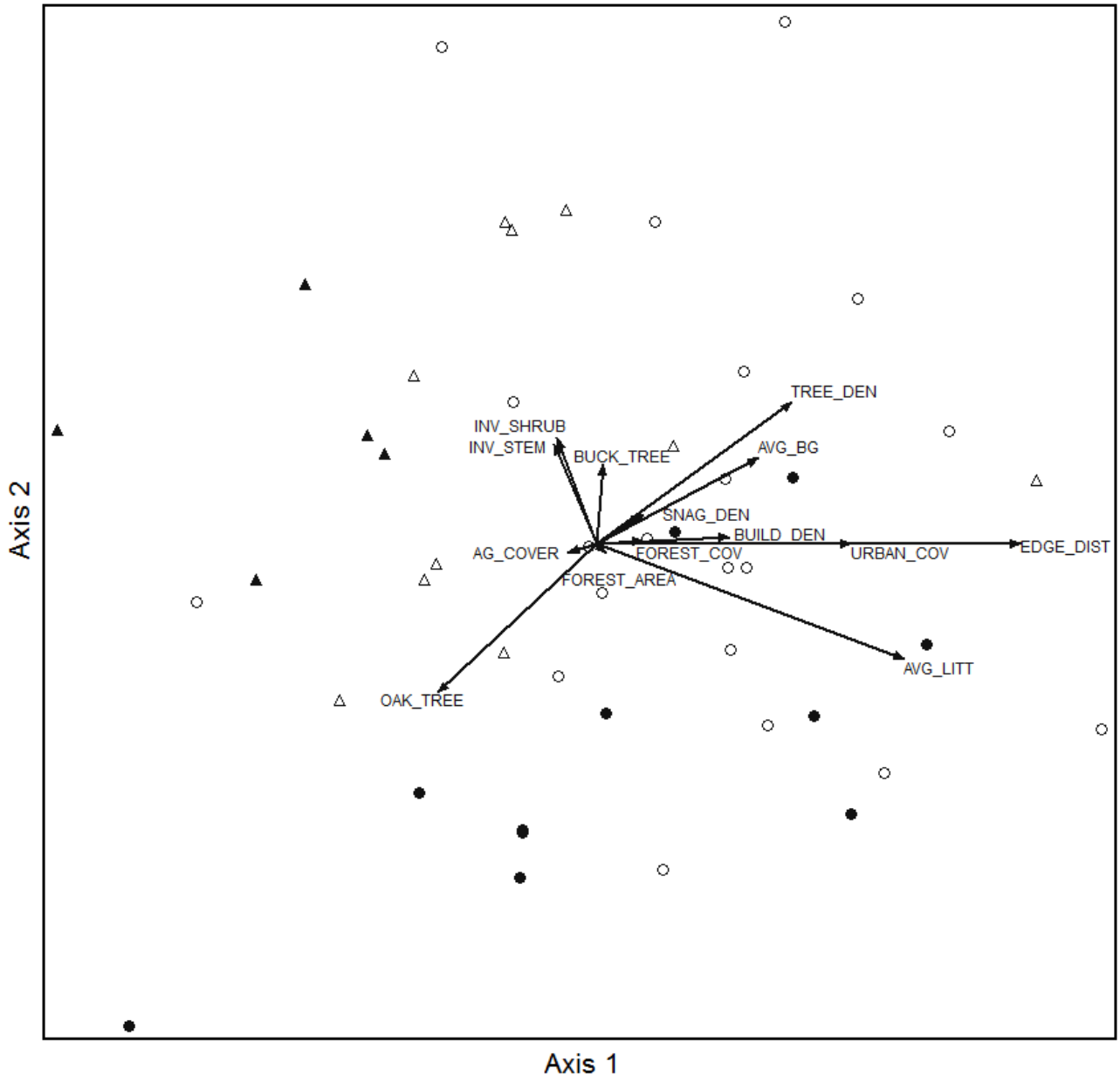
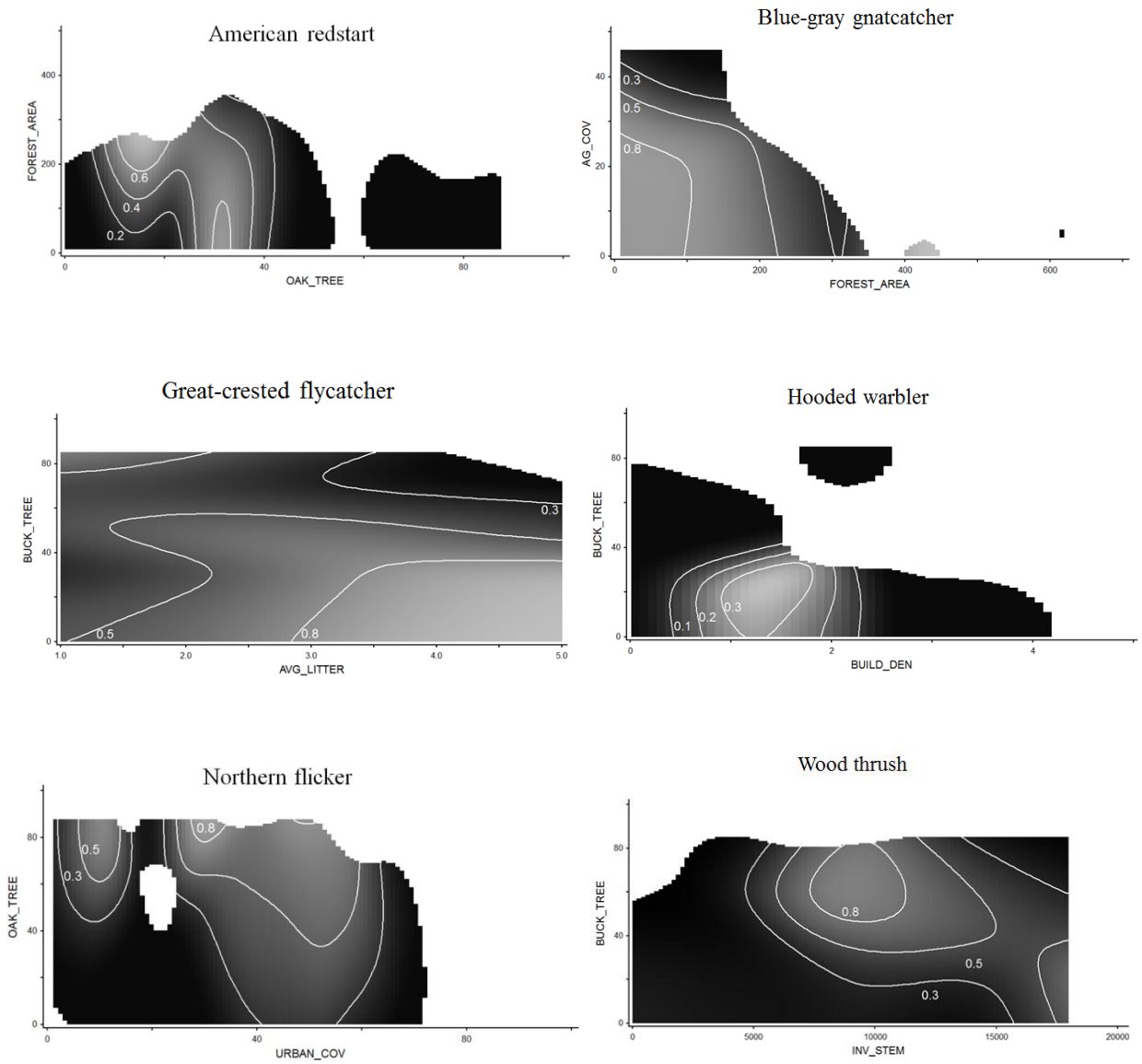

TREE_DEN
INV_SHRUB
INV_STEM
BUCK_TREE
AVG_BG
SNAG_DEN
BUILD_DEN
AG_COVER
FOREST_COV
URBAN_COV
EDGE_DIST
FOREST_AREA
AVG_LITT
OAK_TREE
Axis 2
Axis 1

Figure 4.


American redstart
FOREST_AREA
OAK_TREE
0.6
0.4
0.2
Blue-gray gnatcatcher
AG_COV
FOREST_AREA
0.3
0.5
0.8
Great-crested flycatcher
BUCK_TREE
AVG_LITTER
0.3
0.5
0.8
Hooded warbler
BUCK_TREE
BUILD_DEN
0.1
0.2
0.3
Northern flicker
OAK_TREE
URBAN_COV
0.8
0.5
0.3
Wood thrush
BUCK_TREE
INV_STEM
0.8
0.5
0.3

Chapter 3

Changes in Bird Assemblages Across Forest-Suburb Edges in Northeastern Illinois

Abstract

The impacts of habitat edges on avian communities have received considerable attention, yet few studies have examined how bird populations change on both sides of the interface of distinct habitats. We examined how bird species richness, beta diversity, and community composition changed across forest-suburb edges in the Chicago metropolitan are using replicated point-transects. Additionally, we examined how the distribution of individual bird species differed across these edges. Multivariate analyses revealed that the forest and suburban bird communities were distinct, and that forest bird community composition changed with distance-from-edge, whereas the suburban bird community did not. Species richness was higher in the interior of the forest than the furthest point into suburbia, but near the edge there was slightly higher species richness in the suburbs than in the forest. Generally, the number of species shared between points increased as the distance between them decreased. The majority of bird species were detected in both habitat types, and typical "forest" birds were more likely to venture farther into the suburban habitat than were typical "suburban" birds into the forest. We found that the densities of the most common forest species increased with distance from the edge. Alternatively, the densities of the most common suburban species fluctuated considerably with distance from the edge, and no real trends were revealed. Lastly, we found that the northern cardinal (*Cardinalis cardinalis*) reached its highest densities at locations near the edge. We conclude that distance to the forest-suburb boundary was more influential in structuring avian assemblages in the forest

than in the suburbs. Furthermore, both responses to the habitat boundary and the ability of birds to cross it were species-specific.

Introduction

Understanding the ecological responses of wildlife to habitat edges is critical for comprehending how landscape structure impacts habitat quality, as well as for planning landscape-scale conservation and management efforts (Ries et al. 2004). Habitat edges can have considerable impacts on animal diversity (Johnston 1947, Campi and MacNally 2001), abundance (Lidicker 1999, Kristan 2003), behavior (Haddad 1999, Ries and Debinski 2001), and fitness (Gates and Gysel 1978, Paton 1994). Despite extensive research on wildlife responses to edges, general patterns of edge effects are not always clear (Murcia 1995). A lack of detectable edge response is the most common outcome reported in such studies (Reis et al. 2004), suggesting that numerous species are unaffected by edges (Ries and Sisk 2010). This could be due to the fact that most studies have not been conducted at the spatial scale necessary to detect edge effects in the communities of interest (Laurance 2004).

A better understanding of animal response to edges is needed in metropolitan landscapes, where particularly hard boundaries between urban and natural areas are pervasive. The ability of species to move through or utilize human-dominated areas is a major determinant of functional connectivity at landscape scales (Tischendorf and Fahrig 2000, Walting et al. 2010). Whereas habitat-specialists may be restricted to native core areas because they perceive the urban matrix as impermeable, habitat-generalists can use a variety of land-use types, including developed environments (Gillies and St. Clair 2010). Additionally, some species may only be present within urban areas due to their proximity to their endemic habitats (Antongiovanni and Metzger 2005).

Most edge-related studies focus on only one side of an ecotone (Ewers and Didham 2006). For example, few studies of birds have examined how populations change on both sides of an edge between distinct habitats (Fonseca and Joner 2007). To our knowledge, only two studies have examined how avian assemblages change across boundaries between developed and natural areas, despite the pervasiveness of these interfaces in urbanized landscapes. Catterall et al. (1991) measured habitat use by birds across a eucalypt forest-suburb interface in Brisbane, Australia. These researchers found that there was little movement of either suburban or forest species across the edge, and that large, aggressive species preferred the edge habitats. It is important to acknowledge, however, that this study was conducted at only one large forest for a single year, which limits the applicability of the findings to broader spatial and temporal scales (Catterall et al. 1991). Another study in Australia examined the movements of birds across a suburban-bushland edge, but the transects used across the boundary were only 50 m in length (Hodgson et al. 2007). Overall, findings from this study suggested that avian movement across this edge is dependent on housing density as well as avian feeding guild (Hodgson et al. 2007).

Generally, urban bird communities differ from those in natural remnants, in that they have lower species richness and diversity, higher density, and dominance by a few exotic species (Beissinger and Osborne 1982, Blair 1996, Catterall et al. 2010). This process, known as biotic homogenization, is one in which urbanization promotes the replacement of native species with abundant nonnatives (McKinney 2002). Bird species are often grouped into categories such as "urban exploiters" (species that take advantage of resources associated with urbanization), "suburban adaptable" (generalist species that utilize resources in urban environments such as bird seed or ornamental vegetation), and "urban avoiders" (species that may have large habitat requirements or are sensitive to human-induced changes in the landscape [Blair 1996]).

Urbanization typically favors granivores, omnivores, ground foragers, and generalist species, whereas it selects against foliage gleaners, upper canopy insectivores, bark drillers and gleaners, and specialist species (Chace and Walsh 2006).

We examined how community composition and structure changed across hard edges using replicated point-transects in northeastern Illinois. Specifically, we addressed the following questions: (1) how does avian species richness and beta diversity change across the forest-suburb edge? (2) How do the assemblages differ in terms of composition across the edge, and are the bird assemblages near the abrupt edges intermediate between those further into the forest and the suburbs? (3) How are particular species distributed across the edge? (4) Can particular species be classified as edge-exploiters or edge avoiders?

Methods

Study area

We focused on forest remnants in three Illinois counties (Cook, Lake, and DuPage) located in the Chicago metropolitan area (Fig. 5). These counties are the most populous in Illinois, with more than 6 million residents (U.S. Census Bureau 2010). Land-use in these counties is mostly urban; however large tracts of remnant vegetation remain. Despite the challenges posed to habitat acquisition in the Chicago region, forest preserves and state parks have had great success in protecting and managing natural lands (Miller 2006). The Chicago region encompasses over 80,000 ha of protected lands which include some of the best remaining oak savannas and grasslands in the state (Brawn and Stotz 2001).

Our study focused on forest fragments which were dominated by oak (*Quercus* spp.), and European buckthorn (*Rhamnus cathartica*), although hickory (*Carya* spp.), elm (*Ulmus* spp.), ash

(*Fraxinus* spp.), black cherry (*Prunus serotina*), and maple (*Acer* spp.) were also common. These fragments ranged in size from 54-619 ha. Fragments were mostly surrounded by residential areas, but also open green space (i.e. parks and golf courses) and more urbanized land-uses such as shopping centers and industry.

Site selection

We used ArcGIS 10 (Environmental Systems Research Institute, Redlands, CA) to select the study sites based on two criteria. First, a fragment had to have a forested area large enough to accommodate the transect. Originally we wanted to use longer transects (i.e. 1000 m in length) with > 3 points per-side, but few fragments were large enough. To ensure a reasonable sample size, we settled on transects that were 750 m in length. Second, a preserve had to be next to a suburban area. Twenty-one sites in the Chicago suburbs met these criteria: two in DuPage County, three in Lake County, fifteen in Cook County, and one that spanned the border between Cook and Lake counties.

At each site we established a transect comprised of six avian point count locations, three in a forest and three in an adjacent suburban area (Fig. 5). Points were located 75, 225, and 375 m from a distinct edge separating the two habitat types. All suburban points were placed along roads. Even though concerns have been raised that surveys conducted along roads can be biased (Hanowski and Niemi 1995), roadside counts can generate bird lists that are similar to those generated from off-road counts within the same habitat type (Hutto et al. 1995).

Bird surveys

Birds were surveyed three times annually during the breeding season between late May and early July in 2010 and 2011. We used a standard fixed-radius point count protocol with the radius set at 50 m to avoid double-counting individuals moving among points (Bibby et al. 2000). We conducted 10-minute counts on clear mornings between sunrise and 0930 hours (Bibby et al. 2000). Each year surveys were conducted by two trained observers who rotated among points to minimize potential biases. Prior to each field season, observers underwent a week-long training session to sharpen bird identification and distance estimation skills.

During each survey, we recorded all birds seen or heard as well as distances of birds (in 10-m increments) from the point count location. Fly-overs and birds detected outside the 50-m radius were not recorded. Aerial photographs of the area within 50 m of suburban points were utilized during surveys to provide landmarks and improve distance estimates. This radius typically only included front-yards and houses. We attempted to control for anthropogenic noise by conducting surveys early in the morning when noise was less of an issue. If continuous noise (i.e. lawnmowers or garbage trucks) interrupted a survey, observers stopped and returned to the location at a later time.

Habitat characteristics

We visually estimated percent shrub cover and the number of trees within 50 m of every point. We used a spherical densiometer at each point to estimate percent canopy cover. At forest points, we also quantified the degree of invasion by buckthorn and honeysuckle within the 50-m radius on a scale of 0-2 with 0 representing relatively un-invaded areas, 1 representing "moderately invaded" areas (i.e. locations that were characterized by the presence of some invasives), and 2

representing “heavily invaded” areas (i.e. locations with extremely dense invasive vegetation and many buckthorn trees). Areas receiving a score of 1 had typically undergone some sort of management in the past, whereas areas receiving a score of 2 had clearly received no management attention and were difficult to maneuver through. Lastly, within the 50-m radius of suburban points we recorded the number of bird feeders and buildings. Buildings that were only partially within the 50-m radius were included.

Data analyses

We restricted analyses to bird species that were likely breeding in the area (i.e. migrants were not included). We excluded gulls, raptors, shorebirds, and waterfowl because point counts are not considered a suitable method for these taxa (Bibby et al. 2000). First, we tested for interannual differences in avian abundance using a repeated-measures analysis of variance (ANOVA), with year as the repeated measure and habitat type (suburban or forest) as the main effect.

Species richness was calculated by summing the number of unique species encountered at a particular point over the three visits in each year. Average species richness per point count was calculated as the average number of species detected during a survey each year. We used an ANOVA in the Statistical Analysis System (SAS version 9.2; SAS Institute 1990) to determine if these two species richness measures differed along the point-transects each year. If the ANOVA was significant, multiple comparisons were made with Fischer’s LSD. We conducted this same analysis to determine whether the environmental variables differed among the three distance categories within each habitat type. To test if the measurements degree of invasion and number of bird feeders differed among distance categories we used Fischer’s Exact Test because these environmental variables were discrete.

To examine differences in beta diversity among distance categories, we calculated absolute species turnover for each distance category comparison. Species turnover was calculated as:

$$\beta_A = (S_1 - c) + (S_2 - c)$$

where S_1 is the total number of species detected in the first assemblage, S_2 is the total number of species detected in the second assemblage, and c is the number of species common to both assemblages summed over all three visits in a year (Whittaker 1972). The larger values are associated with fewer shared species.

To determine if bird assemblages differed significantly in terms of their composition (i.e. species present) along the point-transect, we conducted a permutational analysis of variance (PERMANOVA; Anderson 2001, 2005) for each year using PC-ORD version 6 (McCune and Mefford 2011). PERMANOVA conducts an F-test for differences in mean within-group distances among groups and calculates a p-value via permutations (Anderson 2001). If the overall test was significant, we used *a posteriori* pair-wise comparisons to examine which distance categories differed from which.

To examine community dissimilarity among points, we used the unconstrained distance-based ordination technique nonmetric multidimensional scaling (NMDS; Kruskal 1964) in PC-ORD. NMDS arranges sample units in ordination space according to their rank order of ecological distance, so relative inter-point distances reveal the level of similarity between bird communities sampled at those locations. We used the Bray-Curtis distance as a measure of ecological dissimilarity based on its ability to identify ecological gradients (Faith et al. 1987) and because it is less sensitive to differences among rare species. For this analysis and the

PERMANOVA we used presence-absence data because estimates of occurrence are more reliable than abundance estimates when comparing among different habitat types.

Next we examined presence-absence data of all species, except for those that were ubiquitous relative to forest-suburban edges. We pooled these data across years because the birds included in this descriptive analysis did not show significant interannual differences in abundance. Additionally, we highlighted birds that are recognized as species of greatest conservation concern in Illinois (Illinois Department of Natural Resources 2005), and exotic species.

To determine if there were differences in the densities (birds/ha) of particular species among distance categories, we derived density estimates using program DISTANCE 6.0 (Thomas et al. 2009). Point count data were modeled to account for differences in detectability with radial distance from the observer. First we tested for annual variation in species abundances. If there was a significant difference ($p < 0.05$) in the total abundance of a particular species between years, we generated separate detection functions for each year. If year was not significant, we pooled observations across years to increase sample sizes. Typically ≥ 40 observations are needed to obtain reasonably precise density estimates (Buckland et al. 2001), so densities could not be derived for all species. For species with adequate sample sizes, we compared five commonly used detectability models (Buckland et al. 1993). These models were ranked according to Akaike's Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002). We then tested the null hypothesis of equal densities of each species at each distance category using an ANOVA in SAS. Multiple comparisons were made with Fischer's LSD if distance category was a significant factor.

Results

Environmental variables

None of the environmental variables differed among the distance categories in either habitat (forest: canopy cover, F = 0.10, $p = 0.908$; shrub cover F = 0.48, $p = 0.619$; number of trees, F = 0.72, $p = 0.491$; degree of invasion, Fisher's exact test, $p = 0.317$; suburb: canopy cover, F = 0.30, $p = 0.740$; shrub cover, F= 1.06, $p = 0.353$; number of trees, F = 0.23, $p = 0.797$, number of buildings, F = 0.08, $p = 0.928$; number of bird feeders, Fischer's exact test, $p = 0.120$). These results confirm that the edge was indeed abrupt, and that each habitat type was relatively homogenous with respect to these measures. Difference in avian distributions along the point transects were therefore not due to some underlying environmental gradient.

Bird communities

Avian abundances differed between years ($p < 0.01$) and habitat type ($p < 0.01$), but there was no year-by-habitat interaction ($p = 0.56$). Overall, total bird abundance was significantly higher in 2010 than in 2011 in both forest (F= 24.91; $p < 0.01$) and suburban (F = 9.85; $p < 0.01$) habitats. These trends were driven mainly by differences in common and widespread birds such as the American robin (*Turdus migratorius*). Overall, these findings are likely due to the fact that the summer of 2011 experienced a greater amount of precipitation and lower average temperatures than the summer of 2010 (Illinois State Water Survey, Champaign and Peoria, IL). Between May and July in 2010 the mean temperature was 21.2 ºC and the daily max precipitation was 15.6 cm at the Chicago O'Hare weather station. In 2011, these values were 20.4 ºC and 25.5 cm respectively (Illinois State Water Survey, Champaign and Peoria, IL).

We detected 8,103 birds of 65 different species during the course of the study. Of these detections 5,043 were in the suburban habitat, and 3,060 were in the forests. A total of 59 different species were detected in the forest, 46 species were detected in the suburbs, and 40 were detected in both. The American robin was the most abundant species in both habitat types, representing 19.2 % of all forest observations, and 29.3 % of all observations in the suburbs. The house sparrow (*Passer domesticus*) was the second most abundant species in the suburban habitat, representing 21.55% of all suburban observations.

Species richness differed significantly among distance-habitat categories in 2010 ($F = 3.01$, $p = 0.014$), but not in 2011 ($F = 1.97$, $p = 0.088$; Fig. 6A). In 2010, species richness was significantly lower at the two distance categories furthest into the suburbs then at the points furthest into the forest. Species richness was higher in the suburbs (12.10 ± 0.67) than in the forest (10.48 ± 0.63) in 2011 at points nearest the edge, although these differences were not significant. This trend was less pronounced in 2010. Average species richness per point count differed significantly among distance categories in 2011 ($F = 4.15$, $p = 0.002$), but not in 2010 ($F = 1.82$, $p = 0.114$; Fig 6B). In 2011, average species richness was significantly higher at the 75 m suburban distance category than at the 75 m distance category. Generally, the beta diversity correlated positively with the distance between points, whereas the number of species common to both points varied inversely (Table 5). Overall, data collected in 2010 and 2011 showed similar trends and suburban assemblages were more similar among distance categories than were forest assemblages.

The bird assemblages differed significantly among distance categories in 2010 ($F = 12.22$; $p < 0.001$) and 2011 ($F = 11.19$; $p < 0.001$). In addition, differences in the bird assemblages among the distance categories were very similar between years (Table 6). These

comparisons revealed that whereas the bird community did not differ with distance into the suburbs, bird assemblages differed between habitat types and with distance into the forest. The bird assemblage at 375 m into the forest was significantly different than the assemblage at 75 m into the forest in both years. Additionally, there was a significant difference between the 75-m and 225-m forest bird assemblages in 2011.

The 2010 community composition data reached a convergent two-dimensional solution (stress = 20%; Fig. 7A) and the 2011 data reached a convergent three-dimensional solution (stress = 17%; Fig. 7B). For the 2010 NMDS ordination, we display the two axes that had the lowest correlation between ordination distances and distances in the three-dimensional space (McCune and Grace 2002). Distance category centroids followed a pattern similar to that of the point-transect in ordination space, indicating that the closer together distance categories were along the point-transect, the more similar their assemblages in terms of species present. The centroids of the two distance categories nearest the edge were intermediate between those further away from the edge, yet assemblages were clearly distinct between habitat types.

Individual species

A total of 18 species were detected at all six distance categories during the course of the study. The majority of the species were found in both habitat types and could be classified as "suburban adaptable". Several species such as the ovenbird (*Seiurus aurocapilla*) and hooded warbler (*Wilsonia citrine*) were only found in the forest and thus appeared to be "urban avoiders" (Table 7). A total of five species included in the analyses were only detected in the forest habitat, yet only the European starling (*Sturnus vulgaris*), a true "urban exploiter", was detected exclusively in the suburban habitat. Of the three exotic species, the house sparrow and house finch

(*Carpodacus mexicanus*) ventured into the forest habitat, but were only detected at the 75-m points. Species of conservation concern in Illinois were present mostly in the forest fragments, although many were observed in the suburbs. Few species were only detected at points near the edge.

The abundances of just three common species were significantly higher in 2010 than in 2011. These species included the American robin ($t = 4.52$, $p < 0.001$), the blue jay (*Cyanocitta cristata*; $t = 2.07$, $p < 0.039$), and the red-eyed vireo (*Vireo olivaceus*; $t = 3.16$, $p = 0.002$). American robins densities differed significantly among distance categories in the forest in both 2010 ($F = 13.68$, $p < 0.001$) and 2011 ($F = 285.92$, $p < 0.001$; Fig. 8A). Generally, the density of robins in the forest decreased with distance from the boundary. The density of robins also differed among distance categories in the suburbs in both 2010 ($F = 4.81$, $p = 0.008$) and 2011($F = 3.72$, $p = 0.025$; Fig. 8B). Robins reached their highest densities at the 225-m suburban distance category in both years.

The black-capped chickadee (*Poecile atricapillus*) and the Northern cardinal (*Cardinalis cardinalis*) were abundant enough that densities could be estimated across each distance category within each habitat type (Fig. 9). The densities of both the chickadee and the cardinal differed significantly among distance categories in the forest ($F = 584.22$, $p < 0.001$, and $F = 784.12$, $p < 0.001$, respectively; Fig. 9A) as well as the suburbs ($F = 259.93$, $p < 0.001$, and $F = 84.41$, $p < 0.001$, respectively; Fig. 9B). Chickadee densities were lowest at the 375-m distance categories in both habitat types and cardinal densities steadily increased as distance to an edge decreased in both habitat types, indicating that this species is an edge-exploiter.

The densities of eight additional species were compared across the three distance categories in the forest (Table 8). For two of these species, (the red-eyed vireo and the blue jay),

density estimates could only be calculated for 2010, due to insufficient sample sizes in 2011. The densities of red-eyed vireos (F = 125.94, $p < 0.001$), downy woodpeckers (*Picoides pubescens*; F = 1,904.37, $p < 0.001$), red-bellied woodpeckers (*Melanerpes carolinus*; (F = 472.19, $p < 0.001$), eastern wood-pewees (*Contopus virens*; F = 586.67, $p < 0.001$), great-crested flycatchers (*Myiarchus crinitus*; F = 1,000.09, $p < 0.001$), and white-breasted nuthatches (*Sitta carolinensis*; F = 530.89, $p < 0.001$) all differed significantly among forest distance categories. All of these species, except for the blue jay, experienced significant declines as distance-to-the-edge decreased. Blue jay densities did not differ across distance categories (F = 0.17, p = 0.847).

The densities of six different species were compared across the three distance categories in the suburbs (Table 8). The densities of American goldfinches (*Carduelis tristis*; F = 353.16, $p < 0.001$), brown-headed cowbirds (*Molothrus ater*; F = 237.12, $p < 0.001$), house wrens (*Troglodytes aedon*; F = 46.57, $p < 0.001$), mourning doves (*Zenaida macroura;* F = 13.62, $p < 0.001$), and house finches (F = 80.20, $p < 0.001$), all differed significantly among suburban distance categories. Both the mourning dove and the house finch were found in higher densities further into the suburbs. The house wren reached its highest density at the 225-m distance category and both the goldfinch and cowbird reached their lowest densities in the middle suburban category. Densities of house sparrows did not differ significantly among suburban distance categories (F = 2.63, $p = 0.073$).

Discussion

Clearly, forest-suburban edges can strongly impact bird communities. Both community metrics and the multivariate analyses indicated that bird assemblages differed across the boundary. The most notable difference in bird community structure and composition was that between the bird

assemblages within the forest and those within the suburbs. Typically, urban bird assemblages differ quite substantially from those in natural remnants in that they are more homogeneous (i.e. urban areas support fewer species and are dominated by a few exotics; Beissinger and Osborne 1982, Blair 1996, Catterall et al. 2010).

Multiple metrics confirmed that distance-from-an-edge was more important in shaping forest bird assemblages than suburban ones. Bird communities were similar at various distances in the suburbs, whereas differences were detected among forest communities. These differences were likely due to the fact that the forest contained more edge-sensitive habitat-specialists. A related study in Australia found that urban sites both near and far from a forest had similar bird assemblages and neither were comparable to forest assemblages (Catterall et al. 1989). Taken together, these results demonstrate that suburban avifauna are rather uniform throughout. Contrary to our results, Campi and MacNally (2001) found little evidence of change in bird community structure from forest interior to an edge. Their study was considerably different from ours however, in terms of both adjacent habitat type and spatial scale, as it examined avian assemblages along agricultural boundaries in one large (30,000 ha) Australian forest (Campi and MacNally 2001). Despite the major differences in community composition between the two habitat types, our analyses also revealed that while distinct, the bird assemblages nearest the edge were intermediate between those further into either habitat type and generally the closer together on the point transect, the more similar the bird community.

Unlike our findings above, trends in species richness across the forest-suburb boundary were relatively weak. We originally hypothesized that species richness would peak near the edge where species typical of “forest” and “suburban” habitats may be present. Contrary to this prediction however, we found that species richness was significantly higher at the distance

furthest into the forest then at the two distances furthest into the suburbs. The literature supports this result as avian species richness is typically higher in forests than in nearby urban areas (Beissinger and Osborne 1982, Catterall et al. 2010, Shochat et al. 2010). Similar to Loss et al. (2009), we also found that species richness declined slightly in the suburbs as distance from the forest increased. This finding suggests that avian richness within the suburban matrix is enhanced by close proximity to forest remnants. The Loss et al. (2009) study was also conducted in Chicago suburbs, and they concluded that the mere presence of small patches of natural land within the urban landscape can increase avian richness. Furthermore, we found that species richness declined slightly in the forest as distance to the edge decreased, indicating that proximity to a suburban matrix may decrease avian richness with forest remnants.

Another trend that emerged from our species richness analysis was that slightly more species were detected in the suburbs than in the forest at distances nearest the edge and the average number of species detected per point count was significantly higher in the suburbs than in the forest near the edge in 2011. These findings are probably the result of more forest species being likely to cross the edge than suburban birds. The distributions of individual species across the boundary generally support this conclusion, as a greater number of forest species crossed the edge than suburban species. At broader spatial scales, the intermediate disturbance hypothesis is often invoked to explain peaks in species richness in suburban habitats as compared to more natural or urbanized areas (Blair 2001, Germaine and Wakeling 2001). For example, Blair (1996, 2001) found that avian species richness was highest in areas of moderate human development (i.e. residential areas) and attributed this finding to increases in structural diversity (i.e. buildings and vegetation) which could provide more sites for activities such as perching as well as alterations in plant community composition via the introduction of ornamentals.

The distributions of individual species across the forest-suburb boundary shed light on the patterns revealed in our community analyses. Overall, a surprising number of species were present at every distance along the boundary. Most of these birds were abundant generalist species that have adapted well to human activity. Perhaps the most striking finding was that more typical "forest" species tended to cross the boundary and to a greater extent than typical "suburban" birds. Additionally, many species of conservation concern including the wood thrush (*Hylocichla mustelina*) and northern flicker (*Colaptes auratus*) ventured relatively far into the suburbs, suggesting that urbanized areas may not be serving as low-quality for these species as previously thought. Perhaps these habitat boundaries act as zones of adaptation to development for typical "forest" birds. The northern cardinal is an example of a bird that adapted to human-activity in Illinois. Fifty years ago this species was not considered urban, yet now it is found in higher densities in developed habitats than in Chicago forests (Walk et al. 2010). In the winter, this resident species may rely on the resources provided from bird feeding (Atchison and Rodewald 2006).

In our study, only a few forest species such as the ovenbird, an interior-specialist species (Porneluzi et al. 2011), did not cross the interface. These results are in opposition to the findings of Catterall et al. (1991) who concluded that there was a strong tendency for forest species to not venture even 50 m outside the forest. Penetration into the forest by typical "suburban" birds was almost entirely restricted to 75 m. Campi and MacNally (2001) similarly concluded that penetration into the forest by agricultural species was typically restricted to about 100 m. Perhaps this distance represents a threshold beyond which non-forest species rarely venture. These findings suggest that the common perception of urban birds being "adaptable" may be

incorrect. These species may only be adapted to developed areas and may not be good competitors within forests or other natural habitat types.

In terms of species densities most species in the forest exhibited a negative response to the suburban edge whereas no clear trend was revealed for the birds in the suburbs. The densities of these "suburban" species did not follow any consistent pattern and seemed to fluctuate somewhat randomly with distance from the boundary. Perhaps if we had surveyed birds at a distance further into the suburbs or examined these trends at a different spatial scale these weak patterns would disappear. The most abundant bird in this study, the American robin, reached higher densities in the suburban habitat than in the forest. This is likely due to the fact that robins prefer foraging on short suburban lawns (Eiserer 1980), perhaps because they have greater success in hunting worms where grass is sparse as opposed to thick (Heppner 1965). Furthermore, robin densities were highest near the edge within the forest. Robin densities have been shown to decrease with increased distance from homes into natural areas (Odell and Knight 2001).

Several studies have found that certain forest species such as the red-eyed vireo are significantly more abundant in forest interiors than in edge areas (Germaine et al. 1997, King et al. 1997), which supports our finding of more pronounced edge effects in the forest habitat. These birds are mostly tree foraging insectivorous species. Fernández-Juricic (2001) found increased densities of tree foragers in the interior of urban parks, and since insects may be more available in forest interiors than edges due to differences in microclimate (Báldi 1999), perhaps these species are food-limited near edges. Edge avoidance could also reflect changes in unmeasured vegetation structure or increased human disturbance (i.e. anthropogenic noise and

pedestrian traffic). Only the blue jay did not show an edge effect in the forest, a trend that has been noted elsewhere (Kroodsma 1984).

The northern cardinal was an edge-exploiter across the entire forest-suburb boundary. The northern cardinal is often associated with edges and shrubby areas (Halkin and Linville 1999). Several studies have concluded that true edge species are rare. Baker et al. (2002) for example, investigated patterns of bird communities and densities of individual species across naturally occurring wood-heath ecotones in Australia. These researchers found little evidence for entirely ecotonal species. Similarly, a study of two-sided edge responses in forest birds following restoration treatments found that only one species occurred most frequently near the interface (Battin and Sisk 2011). The edge types in these studies differed from ours however, and this difference may have contributed to contrasting results. Edges can attract species due to access to greater food availability in adjacent habitat type (e.g. bird seed in human-dominated landscapes) and nesting sites (e.g. more exotic shrubs for the certain birds to nest in; Murcia 1995).

Conclusions

Results from this study indicate that distance to the forest-suburb boundary was more influential in structuring avian assemblages in the forest than in the suburbs. Few species were unique to one type of habitat, but overall the forest assemblages were unique from the suburban ones in terms of community composition. Species richness generally decreased from both forest-interior toward the edge, and from this edge into the suburban habitat. Additionally, near the forest-suburb interface, residential areas supported slightly greater species richness than the forest habitat, perhaps because typical "forest" species are more likely to cross the edge and venture further into the adjacent habitat type than are typical "suburban" species. Contrary to some

studies, our findings demonstrate that many species responded to the edge. For example, the northern cardinal seemed to be an edge-exploiter across the entire forest-suburb interface, and most species common in the forest responded negatively to the edge. The maintenance of core forest interior habitat would likely benefit several species of conservation concern such as the ovenbird. This finding, combined with the fact that certain species tend to disappear from smaller fragments (Robbins et al. 1989, Blake 1991), indicate that area-sensitivity has major conservation implications, particularly in urbanizing landscapes. Our findings also suggest that suburban habitats may not be as uninhabitable for forest-interior specialists as previously thought, since many species of conservation concern (e.g. the wood thrush) readily crossed the edge, sometimes even as far as 375 m.

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References

Antongiovanni, M., and J. P. Metzger. 2005. Influence of matrix habitat on the occurrence of insectivorous bird species in Amazonian forest fragments. Biological Conservation 122: 441-451.

American Ornithologists' Union. 1983. Check-List of North American Birds, 7th ed., American Ornithologists' Union, Washington, D.C.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26: 32-46.

Anderson, M. J., 2005. PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance. Department of Statistics, University of Auckland, New Zealand. http://stat.auckland.ac.nz. Accessed 11/9/11.

Atchison, K.A., and A.D. Rodewald. 2006. The value of urban forests to wintering birds. Natural Areas Journal. 26:280-288.

Baker, J., K. French, and R. J. Whelan. 2002. The edge effect and ecotonal species: bird communities across a natural edge in southeastern Australia. Ecology 83: 3048-3059.

Báldi, A. 1999. Microclimate and vegetation edge effects in a reedbed in Hungary. Biodiversity and Conservation 8: 1697-1706.

Beissinger, S. R., and D. R. Osborne. 1982. Effects of urbanization on avian community organization. Condor 84: 75-83.

Bibby, C. J., N. D. Burgess, D. A. Hill, and S. H. Mustoe. 2000. Bird Census Techniques. Elsevier Ltd., London, U.K.

Blair, R. B. 1996. Land use and avian species diversity along an urban gradient. Ecological Applications 6: 506-519.

Blair, R. B. 2001. Birds and butterflies along urban gradients in two ecoregions of the U.S. Pages 33-56 in Lockwood, J. L., and M. L. McKinney, eds. Biotic Homogenization. Norwell (MA): Kluewer.

Blake, J. G. 1991. Nested subsets and the distribution of birds on isolated woodlots. Conservation Biology 5: 58-66.

Bliss, C. I., and R. A. Fisher. 1953. Fitting the negative binomial distribution to biological data and note on the efficient fitting of the negative binomial. Biometrics 9: 176-200.

Brawn, J. D., and D. F. Stotz. 2001. The importance of the Chicago Region and the Chicago Wilderness initiative to avian conservation. Pages 509–522 in J. Marzluff, R.Bowman, and R.Donnelly, editors. Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Boston.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Cornwall.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodal Inference: a Practical Information-theoretic Approach, second ed. Springer-Verlag, New York.

Campi, M. J., and R. Mac Nally. 2001. Birds on edge: avian assemblages along forest-agricultural boundaries of central Victoria, Australia. Animal Conservation 4: 121-132.

Catterall, C. P., J. A. Cousin, S. Piper, and G. Johnson. 2010. Long-term dynamics of bird diversity in forest and suburb: decay, turnover or homogenization? Diversity and Distributions 16: 559-570.

Catterall, C. P., Green, R. J., and D. N. Jones. 1989. Occurrence of birds in relation to plants in a subtropical city. Australian Wildlife Research 16: 289-305.

Catterall, C. P., R. J. Green, and D. N. Jones. 1991. Habitat use by birds across a forest-suburb interface in Brisbane: implications for corridors. In: Saunders, D. A., and R. J. Hobbs (Eds.), Nature Conservation. 2: The Role of Corridors. Surrey and Beatty and Sons Pty Ltd, Chipping Norton, NSW, pp. 247-258.

Chace, J. F., and J. J. Walsh. 2006. Urban effects on native avifauna: a review. Landscape and Urban Planning 74: 46-69.

Eiserer, L. A. 1980. Effects of grass length and mowing on foraging behavior of the American robin (*Turdus migratorius*). Auk 97: 576-580.

Ewers, R. M., and R. K. Didham. 2006. Continuous response functions for quantifying the strength of edge effects. Journal of Applied Ecology 43: 527-536.

Faith, D. P., P. R. Minchin, and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69: 57-68.

Fernández-Juricic, E. 2001. Avian spatial segregation at edges and interiors of urban parks in Madrid, Spain. Biodiversity and Conservation 10: 1303-1316.

Finch, D. 1991. Population ecology, habitat requirements, and conservation of Neotropical migratory birds. General technical report RM-205, U. S. Forest Service, Rocky Mountain Forest and Range Experimental Station, Fort Collins, Colorado.

Fonseca, C. R., and F. Joner. 2007. Two-sided edge effect studies and the restoration of endangered ecosystems. Restoration Ecology 15: 613-619.

Friesen, L. E., P. F. J. Eagles, and R. J. Mackay. 1995. Effects of residential development on forest-dwelling Neotropical migrant songbirds. Conservation Biology 9: 1408-1414.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledgling success in field-forest ecotones. Ecology 59: 871-883.

Germaine, S. S., S. H. Vessey, and D. E. Capen. 1997. Effects of small forest openings on the breeding bird community in a Vermont hardwood forest. Condor 99: 708-718.

Germaine, S. S., and B. F. Wakeling. 2001. Lizard species distributors and habitat occupation along an urban gradient in Tucson, Arizona, USA. Biological Conservation 97: 229-237.

Gillies, C. S., and C. C. St. Clair. 2010. Functional responses in habitat selection by tropical birds moving through fragmented forest. Journal of Applied Ecology 47: 182-190.

Greenberg, J. 2002. A Natural History of the Chicago Region. University of Chicago Press, Chicago, IL.

Haddad, N. M. 1999. Corridor use predicted from behaviors at habitat boundaries. American Naturalist 153: 213-227.

Halkin, Sylvia L. and Susan U. Linville. 1999. Northern Cardinal (*Cardinalis cardinalis*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online. http://bna.birds.cornell.edu/bna/species/440/articles/habitat. Accessed 3/1/12.

Hanowski, J. M., and G. J. Niemi. 1995. A comparison of on- and off-road bird counts: do you need to go off road to count bird accurately? Journal of Field Ornithology 66: 469-483.

Heppner, F. 1965. Sensory mechanisms and environmental clues used by the American robin in locating earthworms. Condor 67: 247-256.

Hodgson, P., K. French, R. E. Major. 2007. Avian movement across abrupt ecological edges: differential responses to housing density in an urban matrix. Landscape and Urban Planning 79: 266-272.

Hutto, R. L., S. J. Hejl, J. F. Kelly, and S. M. Pletschet. 1994. A comparison of bird detection rates derived from on-road versus off-road point counts in northern Montana. Pages 104-

111, in C. J. Ralph, J. F. Sauer, and S. Droege, eds. Monitoring bird population trends by point counts. USDA Forest Service General Technical Report PSW-GTR-149. Pacific Southwest Research Station, Forest Service, USDA. Albany, California.

Illinois Department of Natural Resources. 2005. Illinois Comprehensive Wildlife Conservation Plan and Strategy. Version 1.0.

Johnston, V. R. 1947. Breeding birds of the forest edge in Illinois. Condor 49: 45-53.

King, D. I., C. R. Griffin, and R. M. DeGraaf. 1997. Effect of clearcut borders on distribution and abundance of forest birds in northern New Hampshire. Wilson Bulletin 109: 239-245.

Kristan, W. B., A. J. Lynam, M. V. Price, J. T. Rotenberry. 2003. Alternative causes of edge-abundance relationships in birds and small mammals of California coastal sage scrub. Ecography 26: 29-44.

Kroodsma, R. L. 1984. Effect of edge on breeding forest bird species. The Wilson Bulletin 96: 426-436.

Kruskal, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. Psychometrika 29: 115-129.

Laurance, W. F. 2004. Do edge effects occur over large spatial scales? Trends in Ecology and Evolution 15: 134-135.

Lidicker, W. Z. 1999. Responses of mammals to habitat edges: an overview. Landscape Ecology 14: 333-343.

Loss, S. R., M. O. Ruiz, and J. D. Brawn. 2009. Relationships between avian diversity, neighborhood age, income, and environmental characteristics of an urban landscape. Biological Conservation 142: 2,578-2,585.

McCune, B., and J. B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon.

McCune, B., and J. Mefford. 2011. PC-ORD. Multivariate Analysis of Ecological Data. Version 6. MjM Software Design, Gleneden Beach, Oregon.

McKinney, M. L. 2002. Urbanization, Biodiversity, and Conservation. BioScience 52: 883-890.

Miller, J. R. 2006. Restoration, reconciliation, and reconnecting with nature nearby. Biological Conservation 127: 356-361.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution 10: 58-62.

Odell, E. A., and R. L. Knight. 2001. Songbird and medium-sized mammal communities associated with exurban development in Pitkin County, Colorado. Conservation Biology 15: 1143-1150.

Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology 8:17-26.

Poole, A. (Editor). 2005. The Birds of North America Online. Cornell Laboratory of Ornithology, Ithaca, NY. http://bna.birds.cornell.edu/BNA/. Accessed 11/9/11.

Porneluzi, P., M. A. Van Horn, and T. M. Donovan. 2011. Ovenbird (Seiurus aurocapilla), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology. http://bna.birds.cornell.edu/bna/species/088doi:10.2173/bna.88. Accessed 3/1/12.

Reis, L., and D. M. Debinski. 2001. Butterfly responses to habitat edges in the highly fragmented prairies of central Iowa. Journal of Animal Ecology 70: 840-852.

Reis, L., R. J. Fletcher, Jr., J. Battin, and T. D. Sisk. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. Annual Review of Ecology, Evolution, and Systematics 35: 491-522.

Reis, L., and T. D. Sisk. 2010. What is an edge species? The implications of sensitivity to habitat edges. Oikos 199: 1636-1642.

Robbins, C. S., J. R. Sauer, R. S. Greenberg, and S. Droege. 1989. Population declines in North American birds that migrate to the neotropics. Proceedings of the National Academy of Sciences of the United States of America 86: 7658-7662.

SAS Institute. 1990. SAS/STAT user's guide. SAS Institute, Cary, North Carolina.

Shochat, E., S. B. Lerman, J. M. Anderies, P. S. Warren, S. H. Faeth, and C. H. Nilon. 2010. Invasion, competition, and biodiversity loss in urban ecosystems. Bioscience 60: 199-208.

Thomas, L., J. L. Laake, E. Rexstad, S. Strindberg, F. F. C. Marques, S. T. Buckland, D. L. Borchers, D. R. Anderson, K. P. Burnham, M. L. Burt, S. L. Hedley, J. H. Pollard, J. R. B. Bishop, and T. A. Marques. 2009. Distance 6.0. Release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK.

Tischendorg, L. and L. Fahrig. 2000. On the usage and measurement of landscape connectivity. Oikos 90: 7-19.

U.S. Census Bureau. 2010 Census Demographic Profiles. http://2010.census.gov/2010census/popmap/. Accessed 10/31/11.

Walk, J. W., M. P. Ward, T. J. Benson, J. L. Deppe, S. A. Lischka, S. D. Bailey, and J. D. Brawn. 2010. Illinois Birds: a Century of Change. Illinois Natural History Survey Special Publication 31.

Walting, J. L., A. J. Nowakowski, A. J., M. A. Donnelly, and J. L. Orrock. 2010. Meta-analysis reveals the importance of matric composition for animals in fragmented habitats. Global Ecology and Biogeography 20: 209-217.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon 21: 213-251.

Tables

Table 5. Beta diversity between assemblages at different distance categories in 2010 and 2011. The number of species common to both assemblages being compared is in parentheses. Bold-face entries indicate within-habitat comparisons.

		1st community				
	Distance Category	375 m Forest	225 m Forest	75 m Forest	75 m Suburb	225 m Suburb
2nd community	*2010*					
	375 m Forest					
	225 m Forest	**16 (30)**				
	75 m Forest	**20 (26)**	**20 (30)**			
	75 m Suburb	24 (23)	30 (24)	16 (29)		
	225 m Suburb	23 (23)	31 (23)	17 (28)	**15 (33)**	
	375 m Suburb	26 (19)	34 (19)	18 (25)	**14 (26)**	**13 (26)**
	2011					
	375 m Forest					
	225 m Forest	**18 (35)**				
	75 m Forest	**22 (31)**	**19 (34)**			
	75 m Suburb	27 (26)	27 (27)	20 (28)		
	225 m Suburb	29 (22)	29 (24)	22 (25)	**12 (27)**	
	375 m Suburb	30 (20)	30 (22)	23 (23)	**15 (24)**	**11 (24)**

Table 6. Pair-wise comparisons of the bird assemblages (measured with presence-absence data) among the six distance categories in 2010 and 2011, following significant PERMANOVA results (at $p < 0.05$). Numbers are t-values with associated significance (p) in parentheses. Boldface entries indicate significant differences between bird assemblages (at $p < 0.05$).

Distance Category	375 m Forest	225 m Forest	75 m Forest	75 m Suburb	225 m Suburb
2010					
375 m Forest					
225 m Forest	1.06 (0.364)				
75 m Forest	1.70 **(0.004)**	1.06 (0.350)			
75 m Suburb	5.77 **(<0.001)**	4.84 **(<0.001)**	4.52 **(<0.001)**		
225 m Suburb	5.10 **(<0.001)**	4.27 **(<0.001)**	3.82 **(<0.001)**	0.76 (0.742)	
375 m Suburb	4.30 **(<0.001)**	3.69 **(<0.001)**	3.26 **(<0.001)**	1.32 (0.121)	0.91 (0.582)
2011					
375 m Forest					
225 m Forest	0.94 (0.564)				
75 m Forest	1.76 **(0.002)**	1.75 **(0.003)**			
75 m Suburb	5.18 **(<0.001)**	4.78 **(<0.001)**	4.27 **(<0.001)**		
225 m Suburb	4.51 **(<0.001)**	4.13 **(<0.001)**	3.54 **(<0.001)**	1.07 (0.347)	
375 m Suburb	4.03 **(<0.001)**	3.73 **(<0.001)**	3.19 **(<0.001)**	1.36 (0.070)	0.58 (0.902)

Table 7. Distribution of bird species across the distance categories in 2010 and 2011. The X symbol indicates presence and lower-case entries represent presence based on a single observation. The 18 species that were present at all distance categories and irregular visitors (total n < 5) are not included. Bold-face entries are birds recognized as species of greatest conservation concern in Illinois by the State Wildlife Action Plan (Illinois Department of Natural Resources 2005) and italicized entries are exotic species.

Common name	375 m Forest	225 m Forest	75 m Forest	75 m Suburb	225 m Suburb	375 m Suburb
Baltimore oriole	X	X	X	X	X	
Great-crested flycatcher	X	X	X	X	x	
Field sparrow	X	X	x	X	x	
Eastern phoebe	X	x	x	x	x	
Northern flicker	X	X	X	X		x
Scarlet tanager	X	X	X	X		
Acadian flycatcher	X	X	X	x		
Hairy woodpecker	X	X	X			X
Wood thrush	X	X	X			x
Yellow warbler	X	X	X		X	
Eastern towhee	X	X	X			
American redstart	X	X	X			
Hooded warbler	X	X				
Ovenbird	X	X				
Warbling vireo		X	X	X	x	
Savannah sparrow			X	X		
Orchard oriole		X	X			
Tufted titmouse		X	X		x	
European starling				X	X	x
Mourning dove		x		X	X	X
Chipping sparrow	x			X	X	x
Common grackle			X	X	X	X

Table 7 (cont.)

House finch		X	X	X	X
House sparrow		X	X	X	X
American crow	x	X	X	X	X

Table 8. Estimated density (birds/ha ± standard error in parentheses) of birds that were only common in either the forest or the suburban habitat. Due to insufficient sample sizes, the densities of some birds could only be estimated for two distance categories. Superscripts indicate that a variable differed significantly among distance categories (ANOVA, $p < 0.05$); values with different letters are significantly different at $p < 0.05$ (Fischer's LSD).

	Distance Category		
Common name	75 m	225 m	375 m
Forest habitat			
Red-eyed vireo*	0.30 (0.004)[a]	0.47 (0.007)[b]	0.49 (0.010)[b]
Blue jay*	0.40 (0.008)	0.40 (0.006)	0.41 (0.007)
Downy woodpecker	0.10 (< 0.001)[a]	0.12 (0.001)[b]	0.16 (0.001)[c]
Red-bellied woodpecker	0.10 (0.001)[a]	0.11 (0.001)[b]	0.16 (0.002)[c]
Eastern wood-pewee	-	0.14 (0.001)[a]	0.18 (0.001)[b]
Great-crested flycatcher	-	0.12 (0.001)[a]	0.18 (0.001)[b]
White-breasted nuthatch	-	0.10 (< 0.001)[a]	0.13 (0.001)[b]
Suburban habitat			
American goldfinch	0.18 (0.001)[a]	0.13 (0.001)[b]	0.18 (0.002)[a]
Brown-headed cowbird	0.16 (0.002)[a]	0.14 (0.001)[b]	0.20 (0.003)[c]
House wren	0.13 (0.001)[a]	0.15 (0.001)[b]	0.14 (0.001)[c]
Mourning dove	-	0.10 (0.001)[a]	0.11 (0.001)[b]
House finch	-	0.09 (0.001)[a]	0.11 (0.001)[b]
House sparrow	1.33 (0.304)	1.53 (0.217)	0.85 (0.104)

*Densities only estimated for 2010.

Figures

Figure 5. Location of the 21 study sites in northeastern Illinois and a representative point transect illustrative of the study design. Circles surrounding the points represent the 50 m radius around the bird survey locations. Photograph is 2009 high-resolution satellite imagery obtained from the World Imagery basemap in ArcGIS 10 (Environmental Systems Research Institute, Redlands, CA). Scale 1:3,000.

Figure 6. Species richness across the distance categories in 2010 and 2011 represented by (A) total per site, and (B) average per point count. Error bars represent ± standard error. Superscript letters indicate that species richness differed significantly among distance categories (ANOVA, $p < 0.05$); values with different letters are significantly different at $p < 0.05$ (Fischer's LSD). "F" represents forest points, and "S" represents suburban points.

Figure 7. Nonmetric multidimensional scaling (NMDS) of survey points based on avian presence-absence data in both (A) 2010 and (B) 2011. Six levels of the categorical variable distance are plotted as labeled centroids where "F" represents forest points, and "S" represents suburban points. White shapes represent forested points and black shapes represent suburban points. Triangles, squares and circles represent the distance categories 375, 225, and 75 m respectively.

Figure 8. Estimated density (birds/ha ± standard error) of American robins (AMRO) during the breeding seasons of 2010 and 2011 at the three distance categories in (A) the forest habitat, and (B) the suburban habitat. Letters above bars indicate that a variable differed significantly among

distance categories (ANOVA, $p < 0.05$); values with different letters are significantly different at $p < 0.05$ (Fischer's LSD).

Figure 9. Estimated density (birds/ha ± standard error) of Black-capped chickadees (BCCH) and Northern cardinals (NOCA) pooled over both years at the three distance categories in (A) the forest habitat, and (B) the suburban habitat. Letters above bars indicate that a variable differed significantly among distance categories (ANOVA, $p < 0.05$); values with different letters are significantly different at $p < 0.05$ (Fischer's LSD).

Figure 5.

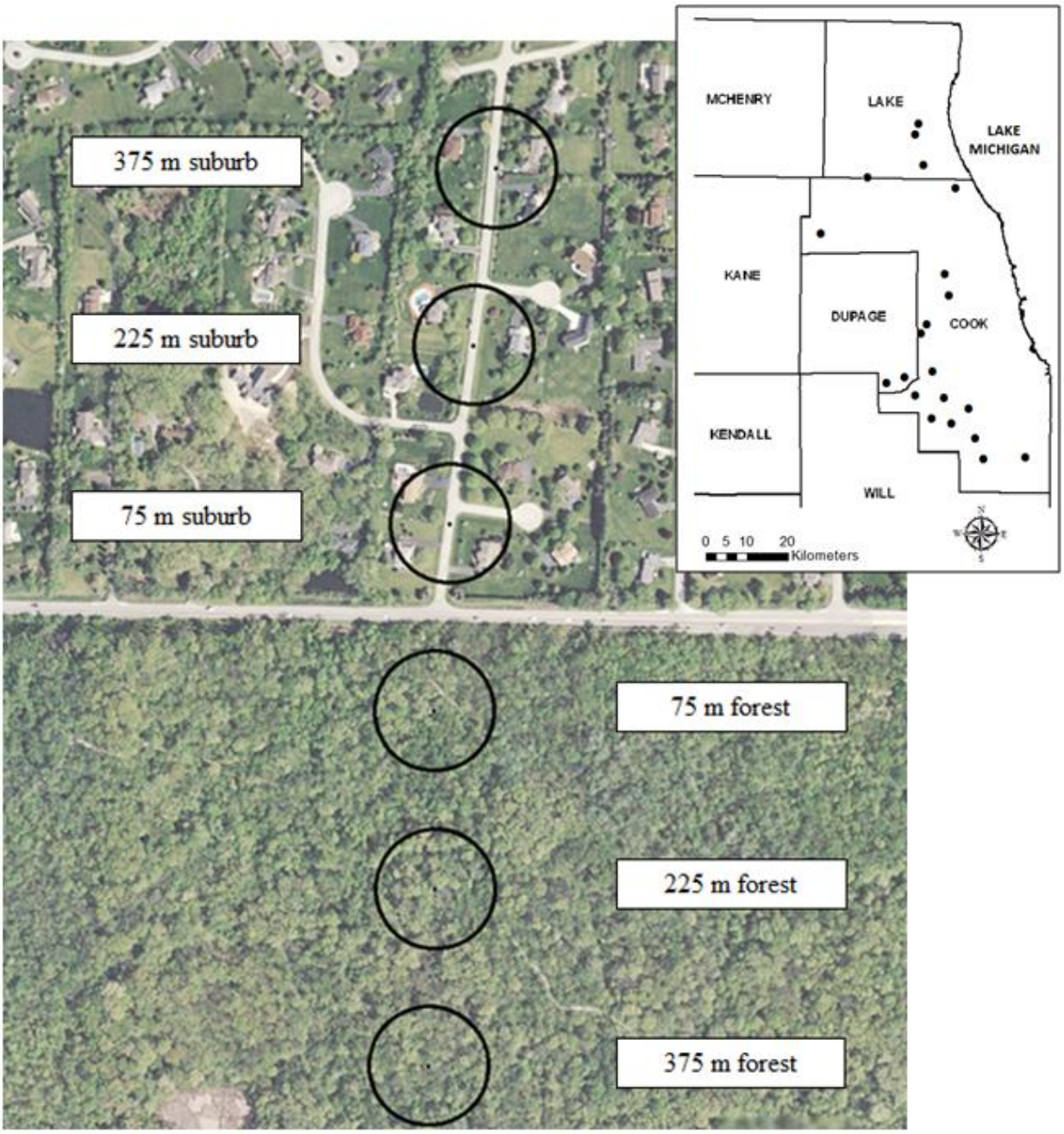
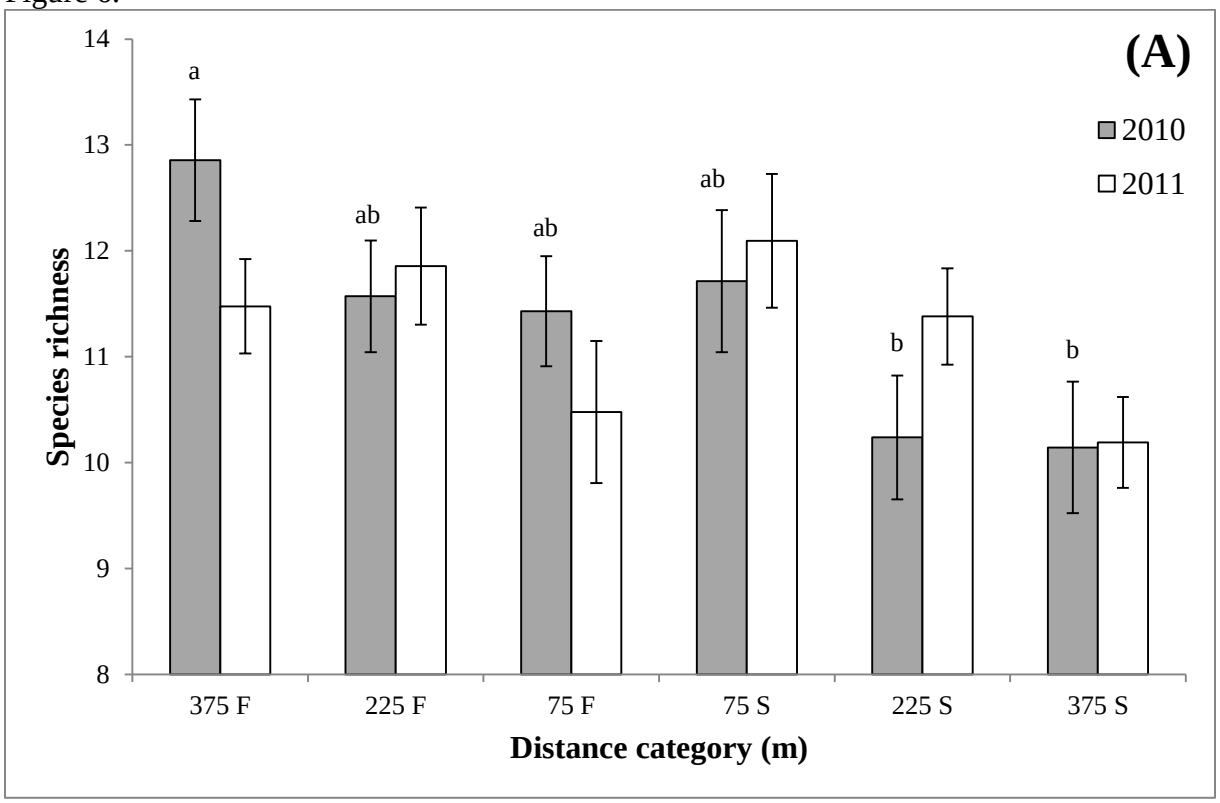

375 m suburb
225 m suburb
75 m suburb
75 m forest
225 m forest
375 m forest
MCHENRY
LAKE
LAKE MICHIGAN
KANE
DUPAGE
COOK
KENDALL
WILL
0 5 10 20
Kilometers

Figure 6.


(A)
2010
2011
Species richness
14
13
12
11
10
9
8
a
ab
ab
ab
b
b
375 F
225 F
75 F
75 S
225 S
375 S
Distance category (m)

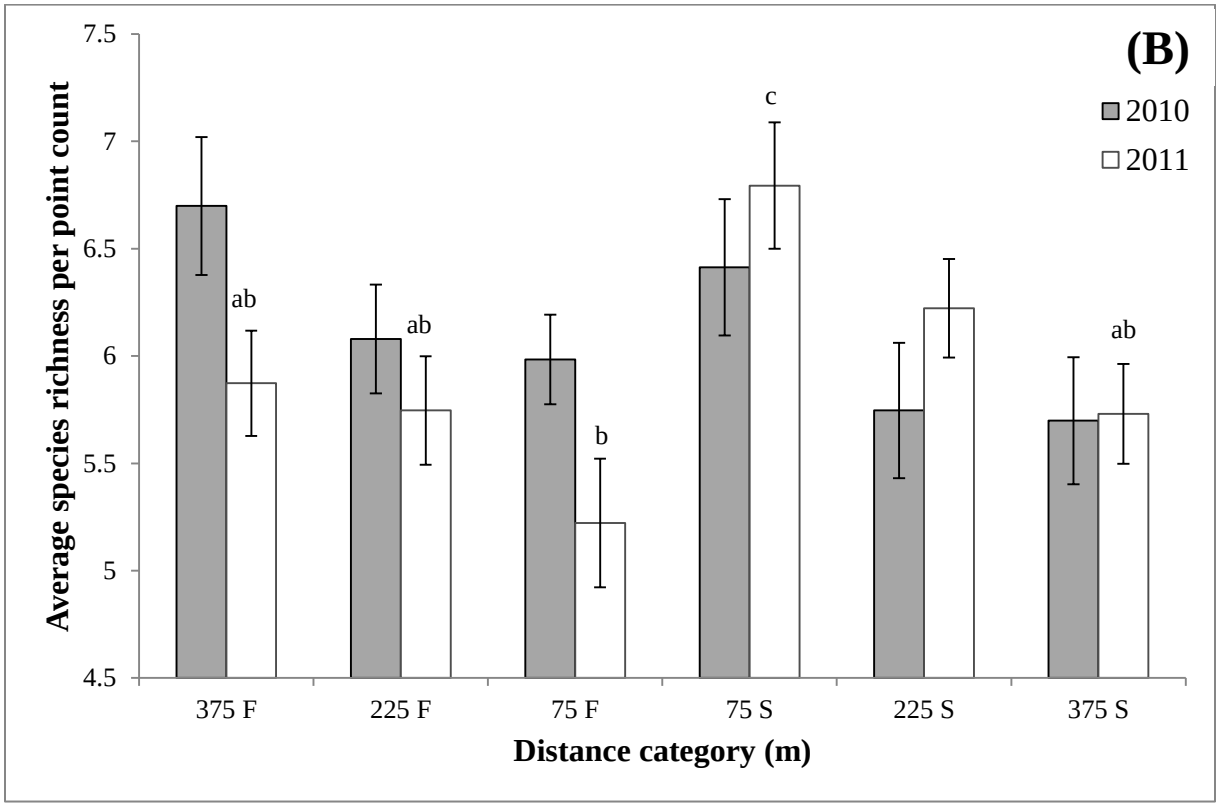
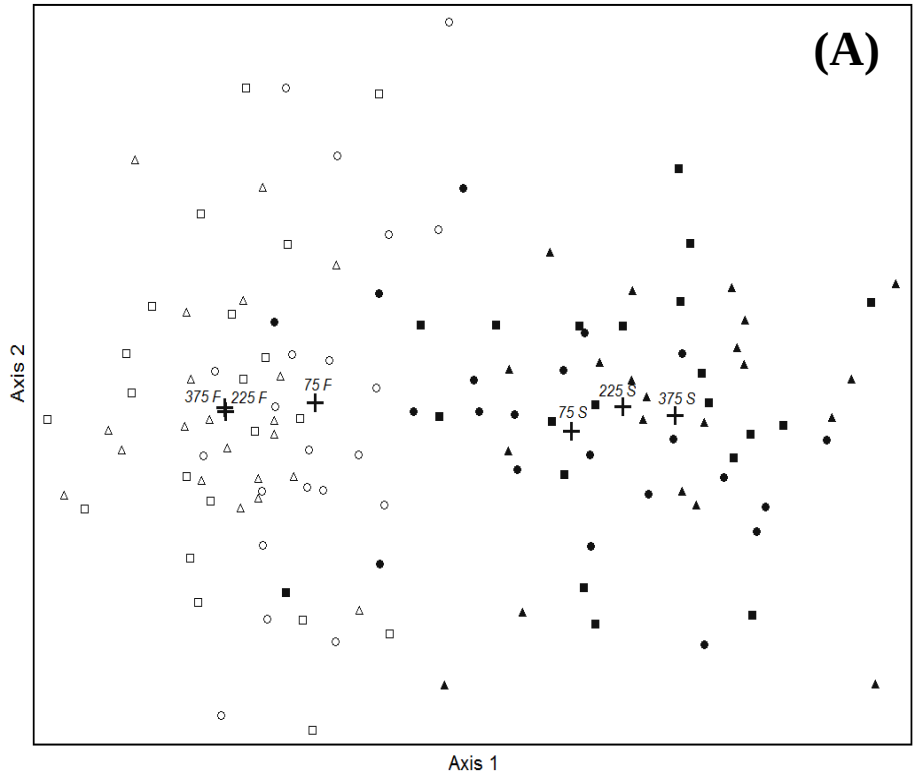

(B)
2010
2011
Average species richness per point count
7.5
7
6.5
6
5.5
5
4.5
ab
ab
b
c
ab
375 F
225 F
75 F
75 S
225 S
375 S
Distance category (m)

Figure 7.


(A)
Axis 2
Axis 1
375 F
225 F
75 F
75 S
225 S
375 S

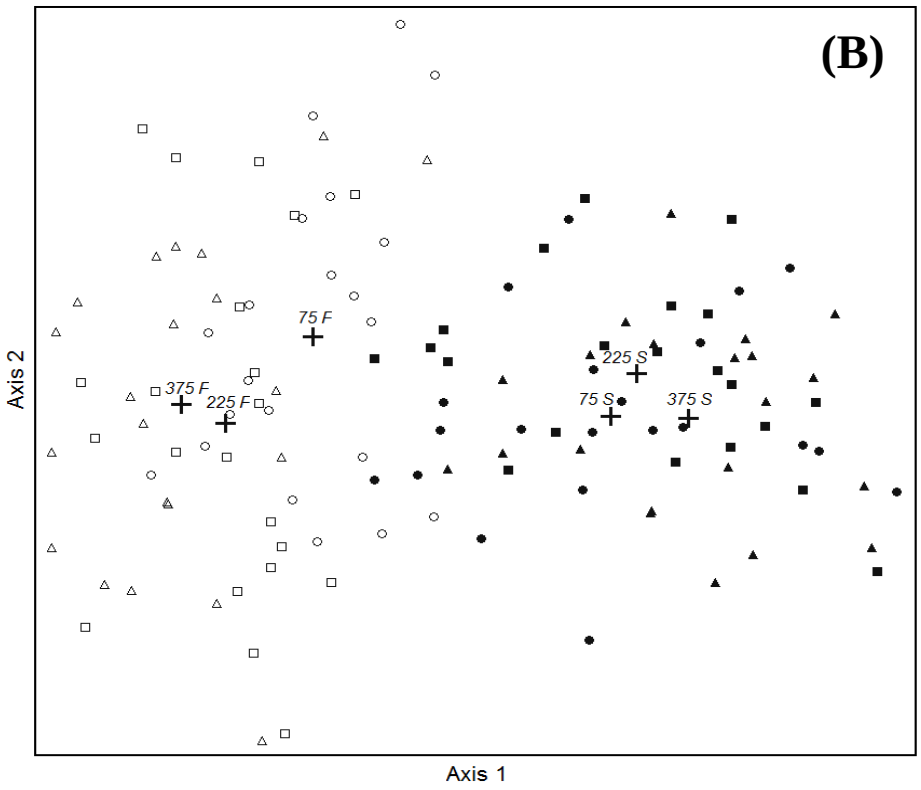
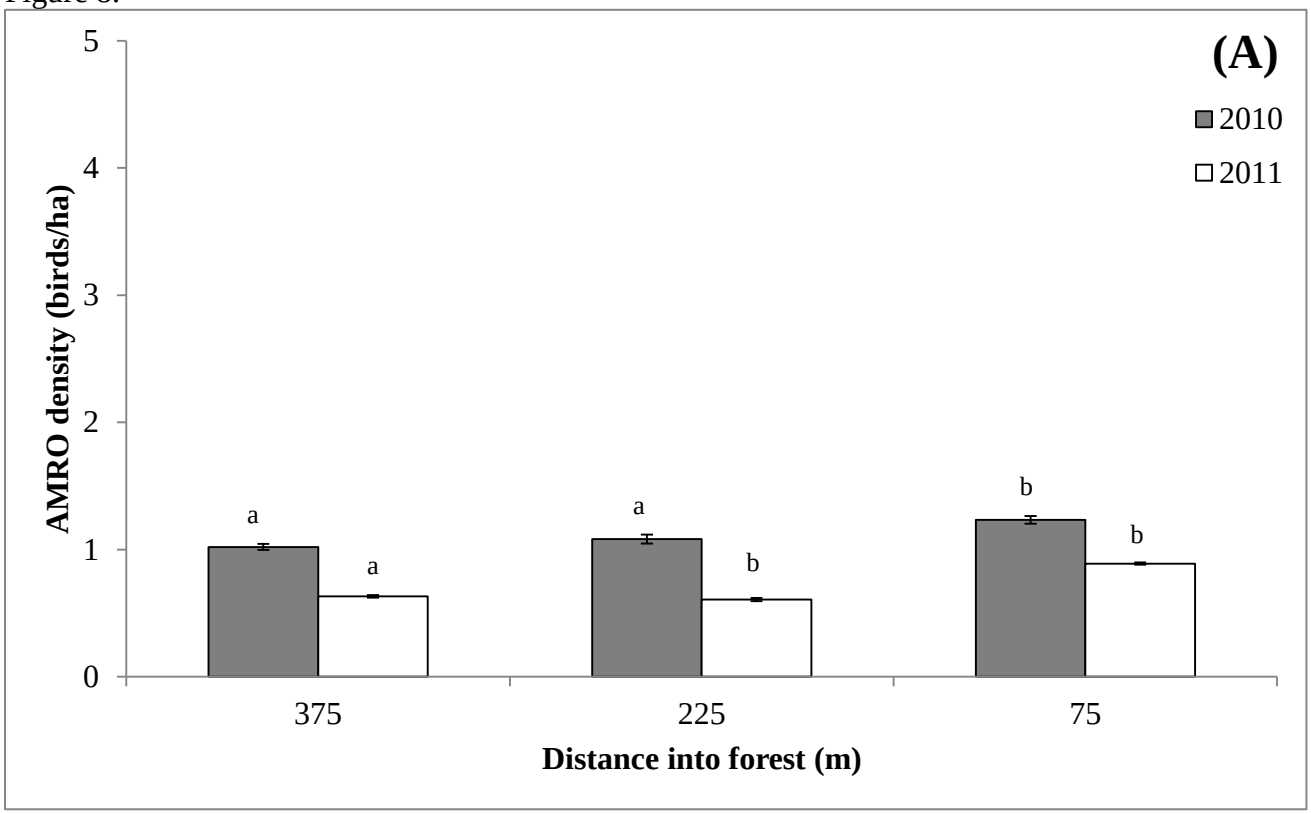

(B)
Axis 2
Axis 1
75 F
375 F
225 F
225 S
75 S
375 S

Figure 8.


(A)
2010
2011
AMRO density (birds/ha)
0
1
2
3
4
5
a
a
a
b
b
b
375
225
75
Distance into forest (m)

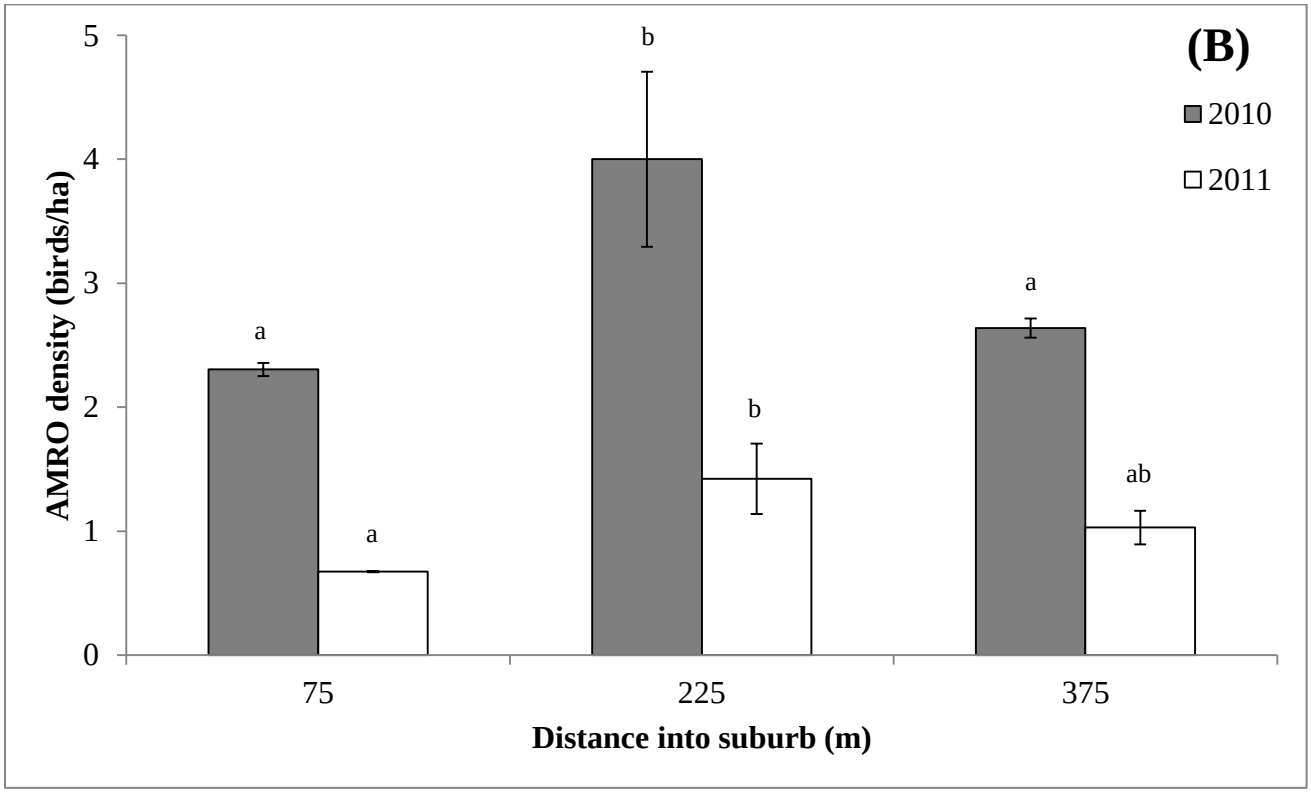
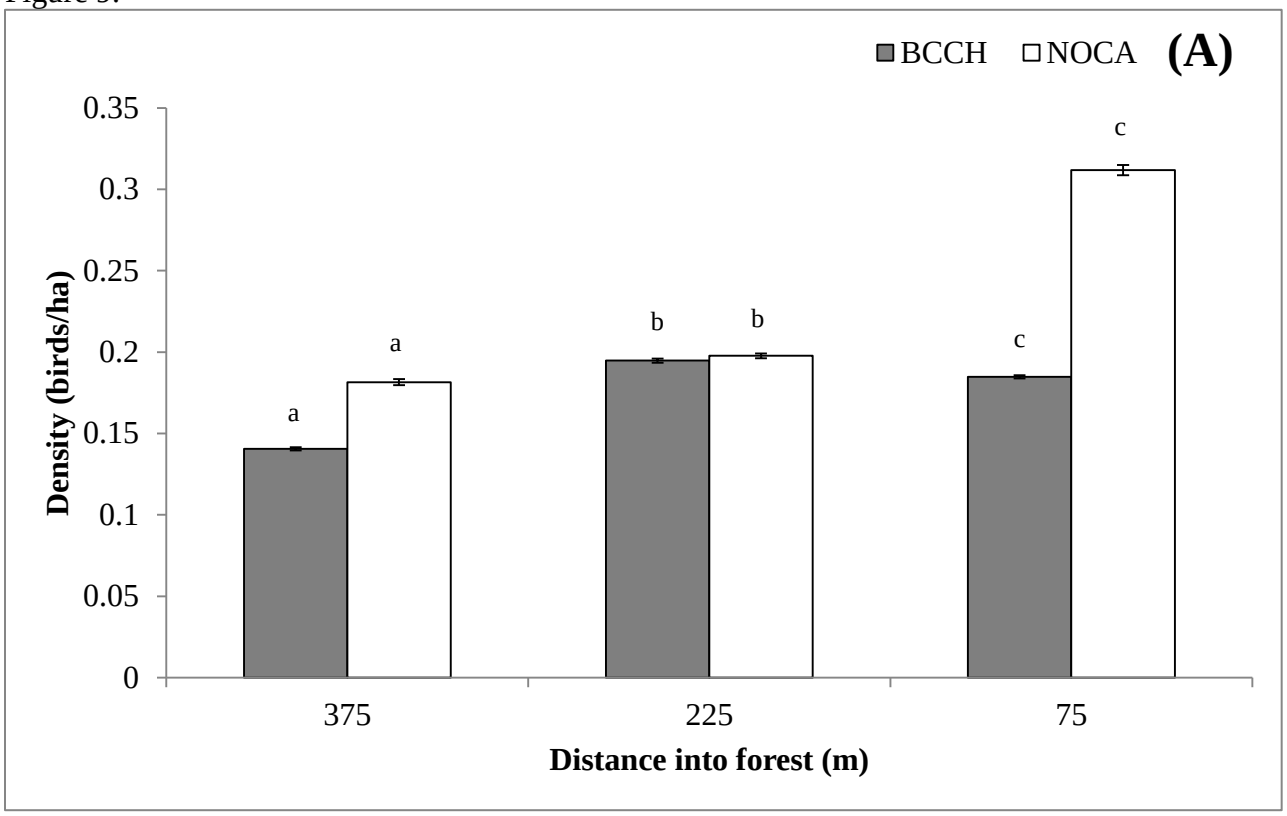
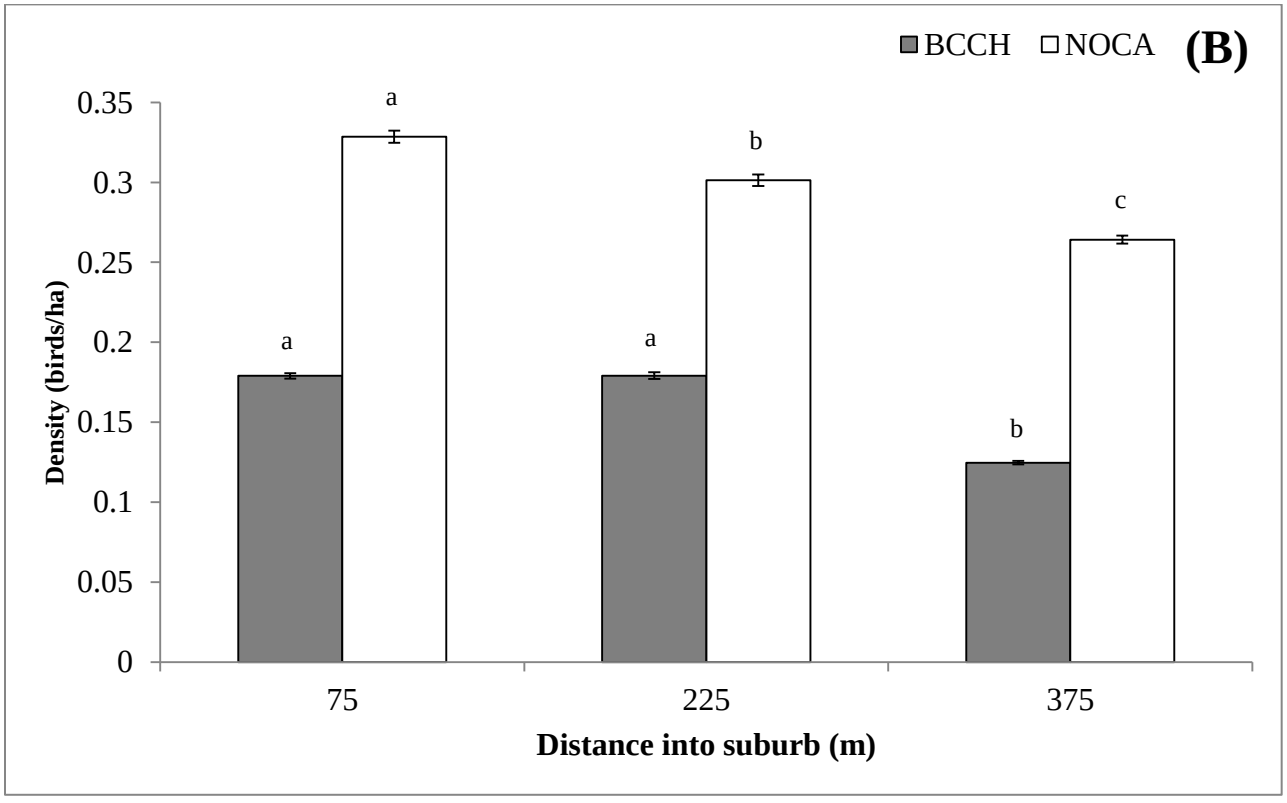

(B)
2010
2011
AMRO density (birds/ha)
0
1
2
3
4
5
a
a
b
b
a
ab
75
225
375
Distance into suburb (m)

Figure 9.


BCCH
NOCA
(A)
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Density (birds/ha)
a
a
b
b
c
c
375
225
75
Distance into forest (m)


BCCH
NOCA
(B)
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Density (birds/ha)
a
a
a
b
b
c
75
225
375
Distance into suburb (m)

Chapter 4

Summary

The primary objective of this research was to gain a better understanding of how bird communities respond to invasions by exotic vegetation and forest-suburban edges within urban landscapes. The main conclusion from the second chapter was that compared to other local and landscape variables, measures of invasive vegetation were weakly correlated with avian community structure. My results did demonstrate however, that both species richness and conservation value decreased with an increase in buckthorn (*Rhamnus cathartica*) tree dominance. I also found that upper canopy nesting and foraging species showed negative responses to shrub invasion, and alternatively, that understory species such as the northern cardinal (*Cardinalis cardinalis*) showed positive responses. Species of conservation concern also responded differently to invasion. For example, while the Great-crested flycatcher (*Myiarchus crinitus*) was more likely to occur in areas with few buckthorn trees, the wood thrush (*Hylocichla mustelina,)* was most likely to occur in areas with mid-to-high levels of invasive stem density and a high proportion of buckthorn trees. While overall the songbird community showed a negative response to exotic shrub invasion, I believe that species-specific responses should be taken into consideration when developing management plans, as certain species may actually benefit from these invasions. I recommend restoring the native shrub understory in addition to invasive shrub removal if possible.

The main finding from the third chapter was that while the forest bird community composition changed with distance from the edge, the suburban bird community remained homogenous throughout. Similarly, the densities of the most common forest species increased with distance from the edge, while the densities of the most common suburban species seemed to

be unaffected by distance from the edge. Species richness was higher in the interior of the forest than the furthest point into suburbia, and near the edge there was slightly higher species richness in the suburbs than in the forest. Additionally, forest birds were more likely than the suburban birds to venture further into their respective adjacent habitat type. Lastly, I found evidence that the northern cardinal could be classified as an edge-exploiter because it reached its highest densities near the boundary in both habitat types. Overall, my findings support the important contribution that forest fragments make to overall avian species richness within urbanized landscapes. This research also suggests that suburban habitats may not be as uninhabitable for forest-interior specialists as previously thought, since many species of conservation concern readily crossed the edge.

Limitations

It is important to note the limitations of our studies. First and foremost, these projects were correlational. While trends were revealed from our analyses, correlation does not imply causation, and an experimental approach would be needed to prove cause-and-effect. I must also stress that I assessed avian habitat quality with point count data. Even though density is usually a good indicator of habitat quality (Bock and Jones 2004), it can be misleading in situations where higher density is not always associated with greater fitness (van Horne 1983). Therefore, in my edge-related study, if the suburban habitat was marginal, then it may have acted as a sink for bird populations in the adjacent forest that contributed dispersing and breeding individuals to the habitat (Donovan et al. 1995). Unfortunately, my study cannot address this issue as I did not measure reproductive success.

A couple of chapter-specific limitations should be recognized as well. For chapter two, all exotic invasive shrub species were grouped together, so if there were species-specific impacts on the bird community we could not detect them. However, any invasive shrub trends were almost entirely attributable to buckthorn, as it was by far the most widespread invasive shrub. Other invasive shrubs such as multiflora rose (*Rose multiflora*) and Amur honeysuckle (*Lonicera maacki*) were only present at a few sites. For chapter three, it is important to note that I only measured a few habitat variables, and most of them were basic visual estimates. Differences that I detected along the forest-suburb boundary therefore could have been due to unmeasured habitat variables. If I had been able to identify and include more transects I could have additionally tested how different guilds of birds or individual species responded to the environmental variables within each habitat type.

References

Bock, C. E., and Z. F. Jones. 2004. Avian habitat evaluation: should counting birds count? Frontiers in Ecology and the Environment 2: 403-410.

Donovan, T. M., R. R. Thompson, III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9: 1380-1395.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. The Journal of Wildlife Management 47: 893-901.

Appendix A

Environmental variables and the corresponding Pearson correlations with nonmetric multidimensional scaling ordination axis scores. See Table 1 for explanation of environmental variable codes. Variables with a Kendall's τ of 0.25 or greater are indicated by bold text.

Variable code	Axis		
	1	2	3
Local			
INV_SHRUB	-0.171	0.284	-0.185
INV_STEM	-0.181	0.269	-0.083
BUCK_TREE	0.081	0.248	-0.034
OAK_TREE	-0.348	-0.340	0.112
TREE_DEN	**0.387**	0.334	-0.045
SNAG_DEN	0.187	0.153	0.007
AVG_BG	**0.356**	0.260	0.037
AVG_LITTER	**0.487**	**-0.302**	-0.122
Landscape			
EDGE_DIST	**0.567**	0.002	0.013
FOREST_AREA	0.089	-0.086	0.013
AG_COV	-0.150	-0.083	-0.154
FOREST_COV	0.191	0.045	0.073
URBAN_COV	**0.444**	-0.032	0.001
BUILD_DEN	**0.315**	0.066	0.013

Appendix B

Pearson correlations of the most abundant bird species with nonmetric multidimensional scaling ordination axis scores. Birds are listed in descending order of total abundance. Variables with a Kendall's τ of 0.25 or greater are indicated by bold text.

Common name	Axis		
	1	2	3
American robin	**0.540**	**-0.566**	0.031
Red-eyed vireo	**0.503**	**0.490**	**0.553**
Northern cardinal	-0.209	**0.686**	-0.342
Indigo bunting	**-0.585**	-0.096	**0.456**
Blue jay	-0.131	**-0.365**	**-0.418**
Eastern wood-pewee	-0.304	-0.029	0.204
Black-capped chickadee	-0.063	-0.015	-0.218
Red-bellied woodpecker	0.279	-0.197	**-0.386**
Downy woodpecker	**0.391**	-0.154	-0.026
White-breasted nuthatch	-0.119	-0.214	-0.028
Blue-gray gnatcatcher	-0.100	**0.311**	0.267
Great-crested flycatcher	0.162	0.263	**-0.382**
Brown-headed cowbird	-0.095	-0.085	-0.024
Red-winged blackbird	-0.358	-0.414	-0.046
House wren	**-0.372**	0.202	0.154
Gray catbird	-0.146	-0.078	**-0.561**
Eastern towhee	**-0.385**	0.064	-0.026
Hairy woodpecker	0.283	0.104	-0.119
Common yellowthroat	**-0.597**	-0.241	-0.006
Cedar waxwing	0.129	-0.018	0.012